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TECHNICAL SERIES, NO. 17, PART II.

U. S. DEPARTMENT OF AGRICULTURE,
BUREAU OF ENTOMOLOGY.
L. O. HOWARD, Entomologist and Chief of Bureau.

CONTRIBUTIONS TOWARD A MONOGRAPH OF THE SCOLYTID BEETLES.

II. PRELIMINARY CLASSIFICATION OF THE SUPERFAMILY SCOLYTOIDEA.

BY

A. D. HOPKINS, PH. D.,
In Charge of Forest Insect Investigations.

ISSUED JANUARY 9, 1915.

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[a] Resigned April 1, 1914.

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U. S. D. A., B. E. Tech. Ser. 17, Pt. II. F. I. I., January 9, 1915.

CONTRIBUTIONS TOWARD A MONOGRAPH OF THE SCOLYTID BEETLES.

II. PRELIMINARY CLASSIFICATION OF THE SUPERFAMILY SCOLYTOIDEA.[a]

By A. D. Hopkins, Ph. D.,
In Charge of Forest Insect Investigations.

INTRODUCTION.

The object of this contribution is to discuss the taxonomy and present a preliminary classification of the families and subfamilies of the scolytoid beetles of the world. The discussion and classification are based on a study of representatives of about 122 described and undescribed genera and about 1,000 species of North America and other countries, in the collections of the U. S. National Museum and certain other museums and institutions of this country.

The types of North American species described by Zimmermann, LeConte, Fitch, Harris, Schwarz, Ulke, and, with a few exceptions, those of other North American authors, have been studied by the writer. Nearly all of the North American species described by Eichhoff are represented in the U. S. National Museum collections by specimens sent by him to the writer and to Dr. C. V. Riley. Many of these specimens are from the type series not only of North American but of many foreign species described by Eichhoff. Central and South America, the West Indies, the Eastern Continent, Australia, and Oceania are represented to a greater or less extent by described and undescribed species, of which 31 genera and 96 species are from Europe, principally from the collections of Eichhoff of Germany, Blandford of England, and Villard of France.

The material in the forest insect collections of the Bureau of Entomology and the West Virginia Agricultural Experiment Station, collected by the writer and his associates, includes nearly all of the described North American species and in addition a large

[a] See Hopkins, A. D. List of generic names and their type-species in the coleopterous superfamily Scolytoidea. Proc. U. S. Nat. Mus., vol. 48, No. 2066, pp. 115–136, December 16, 1914.

number of undescribed species and a great amount of new biological material. With this amount of material at hand and a special study of this group of insects extending over a period of twenty years, the writer feels justified in proposing a revised classification and in defining the characters which it appears to him are of special taxonomic importance.

In presenting the preliminary classification of the Scolytoidea the author does so with no idea of criticising the systems proposed by other authors. The whole presentation is simply to stand as the writer's interpretation of the characters and characteristics represented by the material before him, and to serve, so far as it may, as a step in the evolution of artificial systems of classification toward the ideal or natural. Each comprehensive system of classification proposed since that of Linnæus has contributed something toward the evolution of better systems. Some of them have been progressive, others in part retrogressive, and a few have been revolutionary in their character. But, as in most conflicts of opinion, general progress results. Therefore those investigators of the present and the future who, without prejudice as to any opinion or theory, can sift out the true from the erroneous in that which has been published, and add new truths from their own observations, will make the most rapid progress toward the attainment of the ideal.

The anatomical investigations conducted by the writer and outlined in Part I of this bulletin have revealed heretofore unrecorded facts relating to structural characters, which, in connection with a greatly increased knowledge of the physiological characteristics of the stages of development and of the habits, host relations, and distribution of described and undescribed forms, seem to warrant a somewhat different classification from those proposed by other writers.

It seems that a study of the facts as revealed by modifications in morphological characters and physiological characteristics of existing forms, without any attempt to explain their origin or phylogeny, will lead to a more correct interpretation of natural affinities than any amount of speculation on hypothetical ancestral forms from which present species may have evolved. Indeed, it would seem that we have, in the progressive modification of the more fundamental and dominant characters and characteristics, a better taxonomic basis on which to correlate the characters and construct a so-called natural system than can be found in those characters which are subject to special modification through similar use and influences of environment.[a]

[a] In this connection see Part I of this bulletin, p. 25, second paragraph, and pp. 67–68.

POSITION OF THE SCOLYTOIDEA.

The contrasting characters which indicate the position of the superfamily Scolytoidea in the order Coleoptera are as follows:

Order COLEOPTERA.

Maxilla undivided, the palpi rigid and with not more than three joints; larvæ legless.....Suborder Rhynchophora.
Maxilla divided, more or less flexible, and with a flexible palpus, usually 4-jointed; larvæ rarely without legs.....All other Coleoptera.

Suborder RHYNCHOPHORA.

Head without prominent rostrum or beak and the submentum never produced into a gular peduncle.....Superfamily Scolytoidea.
Head usually with prominent rostrum or beak and the submentum always more or less produced into a gular peduncle.....All other Rhynchophora.

It is evident to the writer that, in consideration of the extremes in morphological characters to be found in the order Coleoptera, the superfamily Scolytoidea occupies a position opposite to that of the Carabidæ, and that in the Rhynchophora it occupies an opposite position to that of the Apionidæ.

It seems desirable to place the Scolytoidea first in the classification of the Coleoptera, not because of any theory as to their origin or phylogeny but because their elements of structure seem to form a better and more correct basis from which to proceed in the interpretation of the progressive modification of the characters which serve to distinguish the major and minor divisions and groups. Such a method should not conflict with other methods because it should make little difference whether we begin with the Scolytoidea or the Carabidæ. If the interpretation of the progressive modifications and natural relations is correct, the relative positions of the various groups will be the same, or similar. It is simply a matter of choosing between the two directly opposite methods to attain the same result and of adopting the one which seems to be more in accord with the natural course of change or evolution from one extreme to the opposite.

If we begin with the scolytoid beetles we find throughout the suborder Rhynchophora two dominant or constant characters, namely, the rigid maxillæ and the legless larvæ. We find also certain changeable characters repeatedly paralleled in the various major and minor groups, and that the general progressive modification of these characters, as, for example, the tendency toward a prolongation of the head, represents a separate and greatly diverging line of morphological expression or evolution from that prevailing in the other divisions of the Coleoptera.

In the other divisions of the Coleoptera the divided maxilla, with flexible palpi, and the legged larvæ are the prevailing and more domi-

nant characters. Here, again, there are a number of changeable and frequently parallel characters, the progressive modification of which shows many diverging lines toward the extreme, as, for example, the greatest development of jointed and differentiated appendages[a] in the larvæ, the large size, the odd shapes, and the extraordinary elements of structure and habit.

It is evident that the scolytoid beetles could not have been derived from the highly differentiated carabids or scarabæids and that these groups could not have been derived from any existing group of the Rhynchophora. It is also evident that the species in the two primary divisions of the Coleoptera which may be the nearest representatives of their primitive ancestors are themselves so highly differentiated from one another and from ancestral forms of Coleoptera that they can not be recognized, or, if they could, they would be of little or no use as a basis for speculation on the origin and evolution of the order; then, too, we have no material in fossils on which to base a reliable hypothesis, because only the highly specialized forms have been preserved. Therefore we must rely on facts as they exist and endeavor to discover and interpret the elements of distinction and relationship which have survived in the course of their evolution, under the influence of natural selection, dominant differentiation, and progressive and parallel evolution. The writer's interpretation of these facts, so far as they apply to morphological characters and the distinction of groups and species, will be expressed in the tables of families, subfamilies, genera, and species, in the succeeding contributions toward a monograph, as will also the progressive modification of characters indicative of the lines of divergence from one extreme toward the opposite.

GENERAL ANATOMY.

The discussion, illustrations, and terminology of the anatomical elements of *Dendroctonus* given in Part I of this bulletin will serve as a basis for comparing the anatomy of representatives of other genera. The writer has made a detailed study of the entire anatomy of only a few representatives of other genera, but the more important elements of the external and internal anatomy of representatives of all of the genera in the local collections have been studied, involving the preparation of over 1,200 microscope slides. This, together with the work of other investigators, notably Lindemann, Nüsslin, Fuchs, and Eichhoff, gives us a basis for a somewhat comprehensive view of the subject. There remains, however, an immense amount of anatomical work to be done before a knowledge of the subject is anything like complete.

[a] The writer holds that it is by no means proven that larvæ with jointed appendages are more primitive than those without such appendages.

TAXONOMY.

MORPHOLOGICAL CHARACTERS.

The principal morphological characters adopted by the writer to distinguish the families, subfamilies, and genera, and the major and minor divisions of each are to be found in the external anatomy of the imago. However, some consideration has been given to the location of correlated characters in the internal anatomy and in the physiological characteristics of the different stages of development from the egg to the imago.

It has seemed to the writer that in order to have a classification which would indicate natural positions and lines of modification, and at the same time be simple and practicable, we should endeavor to locate and utilize, as far as possible, external characters which are readily available for examination by a hand lens or the microscope without serious mutilation of the specimens by those who make use of the systematic tables and descriptions. The small size of most of the scolytoid beetles renders it difficult and tedious to examine the minute and obscure elements of the external and internal anatomy, such as the mouthparts and the digestive and sexual organs. It is very important, in fact essential, that the taxonomist should study in detail, and comprehensively, the various elements of external and internal anatomy in order to have a broad basis for his conclusions, but the general student and investigator should not be required to go to such extremes in order properly to interpret the conclusions. Therefore it has been the object of the writer to conform to the simple method of expression rather than to that involving a complexity of detail.

The principal character-bearing parts of the external anatomy which appear to serve as the best taxonomic guides toward a natural system of classification are mentioned in the following pages merely as a basis for the preliminary classification, which is subject to revision in the more detailed treatment of the several subfamilies.

SUPERFAMILY CHARACTERS.

The superfamily is at once separated into two primary divisions by the relative length of the first tarsal joint, and the subdivisions, sections, and families are distinguished by characters of the tibia (Pl. IX). It is interesting to note that while the most dominant character is found in the first joint of the tarsus, the modification of this joint within the families, subfamilies, and genera is of minor importance. The same, to a lesser degree, may be said of the tibia, in which the character of the apical angles is constant within each subdivision of the superfamily but the modification of these angles

throughout the minor groups to the species, except in a few cases, is of little or no importance.

The complete opposition in the characters of the apical angles of the tibia, as shown in the subdivisions, is of special interest. There is no apparent explanation on any theory of use or natural selection, but it does appear to signify widely diverging lines of descent in which this reversed element in the two subdivisions has remained as the dominant and distinctive character.

FAMILY CHARACTERS.

In the classification of the families Ipidæ and Scolytidæ into subfamilies the principal characters used to distinguish the divisions are found in the head (2)[a], pronotum (4), and tarsi (2).

The subdivisional characters are found in the antennæ (2), tibia (2), and abdominal sternites (2).

The sectional characters are found in the antennæ (2), eyes (2), pronotum (2), tibia (4), and form of body (2).

The subfamily characters are found in the pronotum (4), antennæ (2), seventh abdominal sternite (2), elytra (2), and third tarsal joint (2).

It will be seen that in the classification of the two families into subfamilies the principal characters are found in the head (8), pronotum (10), and tibia (7).

SUBFAMILY CHARACTERS.

In the classification (in manuscript) of the 16 subfamilies of Ipidæ and Scolytidæ into genera the principal character-bearing parts for the divisions, subdivisions, and sections are as follows:

Divisions: Head (1), antennal club (3), funicle (3), eyes (4), epistoma (2), maxilla (1)—total for head (14); pronotum (5), tarsi (3), and elytra (2).

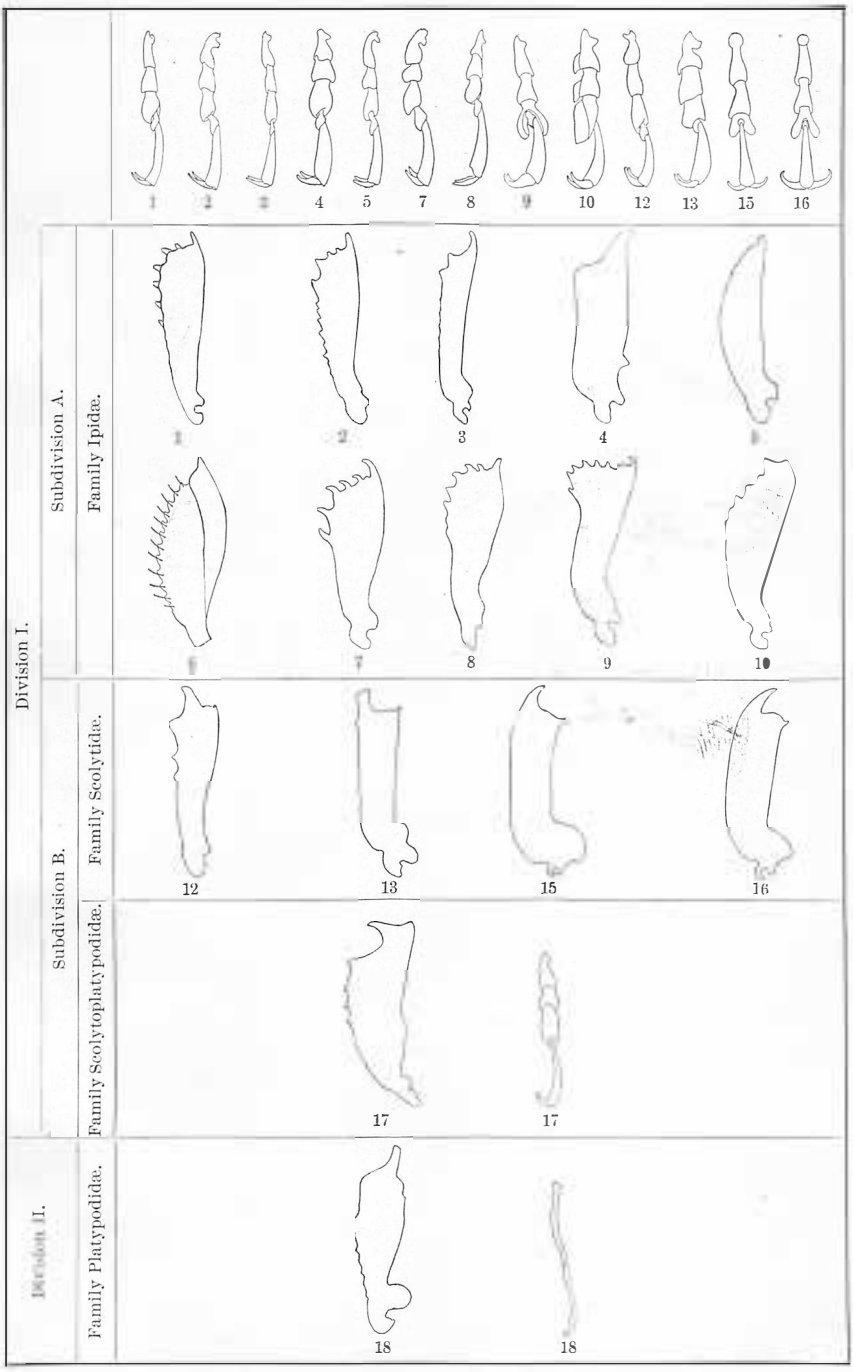
Subdivisions: Antennal club (5), eyes (4), funicle (2), epistoma (1), maxilla (1)—total for head (13); third tarsal joint (2), anterior coxæ (3), seventh abdominal sternite (2), and pygidium (2).

Sections: Antennal club (4), funicle (2), eyes (1)—total (7).

It will be seen that in the classification of the subfamilies the characters are found in the head (35), tarsi (7), pronotum (5), elytra (4), coxæ (3), seventh abdominal sternite (3), pygidium (2), and tibia (1).

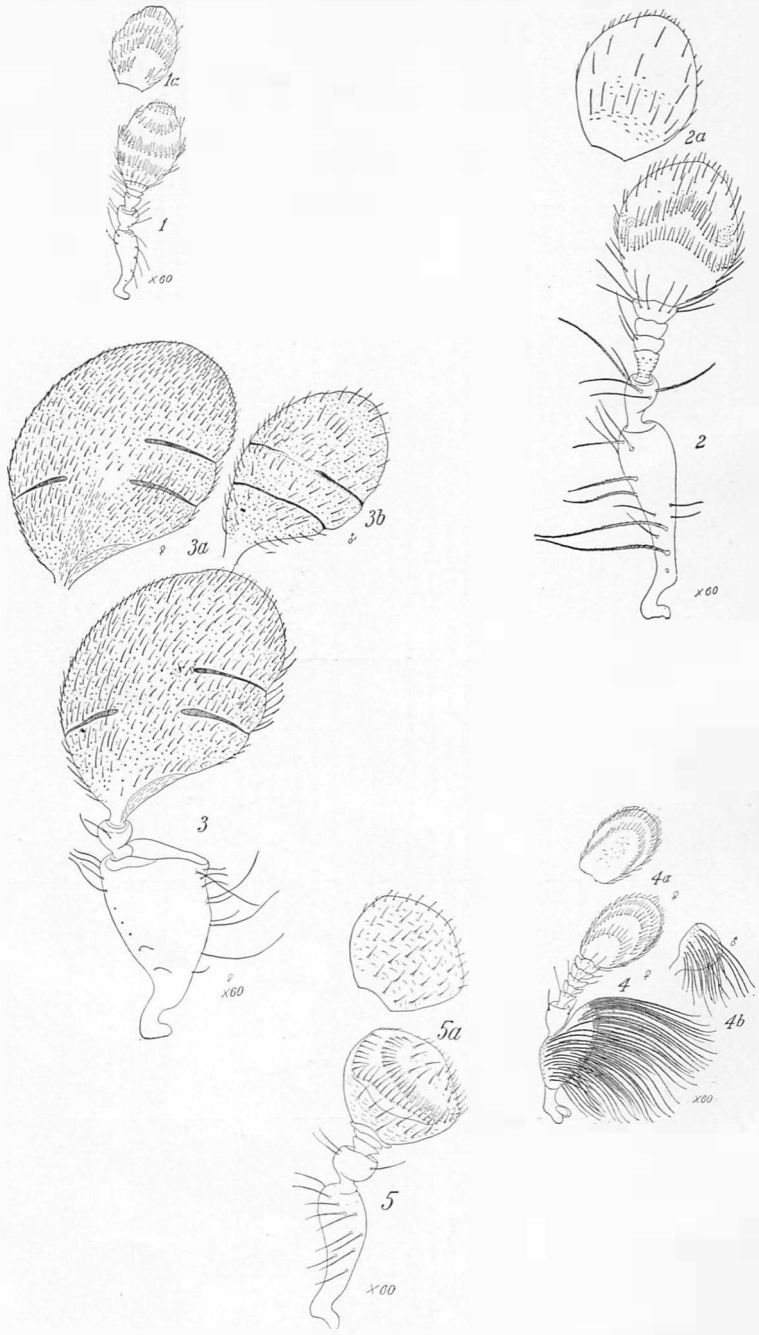
Subsections and series to genera: The dichotomous characters of the subsections and series and the distinctive characters of the genera are as follows: Antennal club (138), funicle (110), scape (7)—total for

[a] The number following the name of a structure indicates the relative importance or the number of times it figures in the dichotomy.



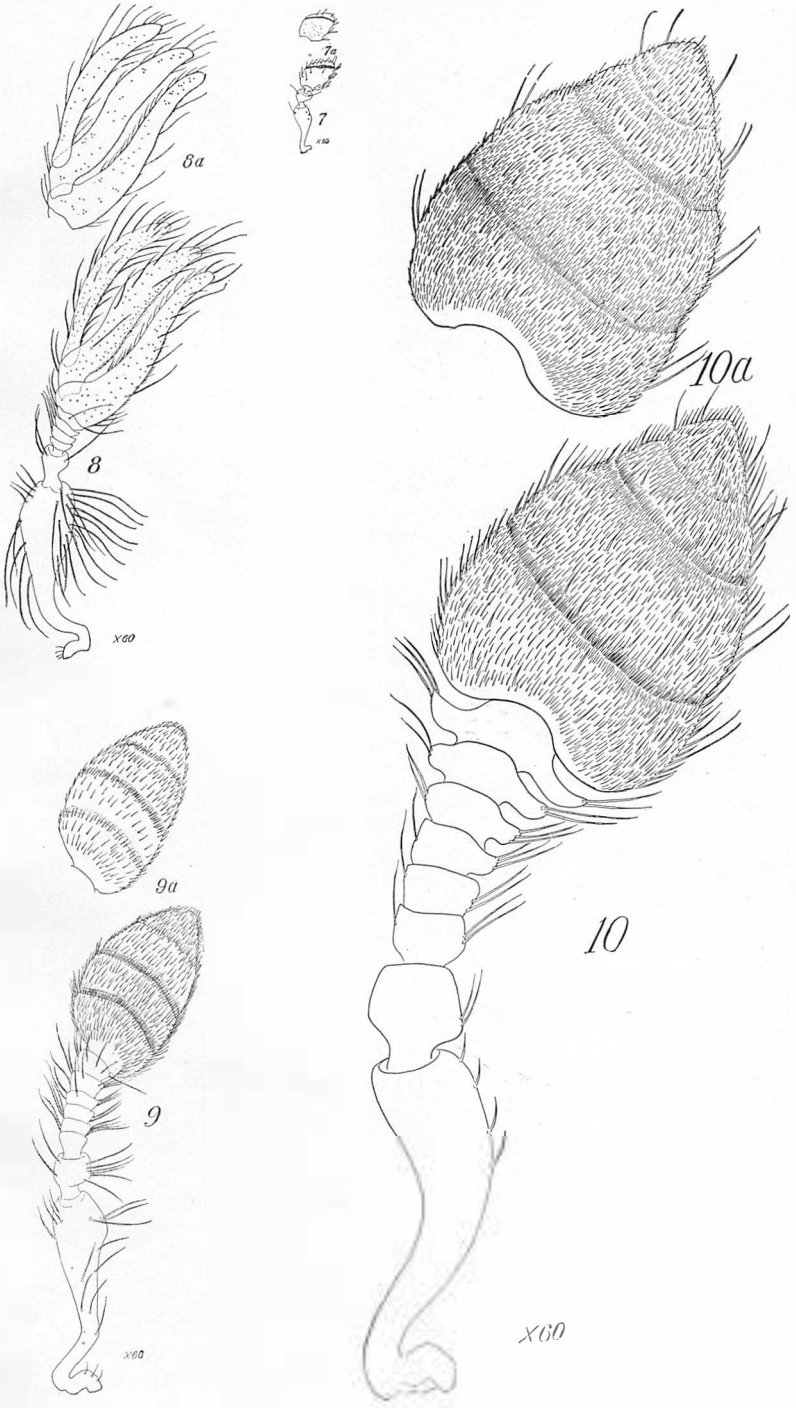
TYPICAL TARSI AND TIBIÆ OF THE SUBFAMILIES OF SCOLYTOIDEA.

Fig. 1.—Cryphalinæ (*Cryphalus asperatus*). Fig. 2.—Ipinæ (*Ips typographus*). Fig. 3.—Corthylinæ (*Corthylus columbianus*). Fig. 4.—Micracinæ (*Micracis suturalis*). Fig. 5.—Webbinæ (*Webbia dipterocarpi*). Fig. 6.—Xyloctoninæ (*Xyloctonus scolytoides*) (adapted from Eichhoff). Fig. 7.—Crypturginæ (*Crypturgus pusillus*). Fig. 8.—Phlœotribinæ (*Phlœotribus oleæ*). Fig. 9.—Hylesininæ (*Hylesinus crenatus*). Fig. 10.—Phlœoborinæ (*Phlœoborus rudis*). Fig. 12.—Hexacolinæ (*Hexacolus* sp.). Fig. 13.—Bothrosterninæ (*Bothrosternus sculpturatus*). Fig. 15.—Camptocerinæ (*Camptocerus æneipennis*). Fig. 16.—Scolytinæ (*Scolytus scolytus*). Fig. 17.—Scolytoplatypodinæ (*Scolytoplatypus* sp.). Fig. 18.—Platypodinæ (*Platypus cylindrus*). (Original.)



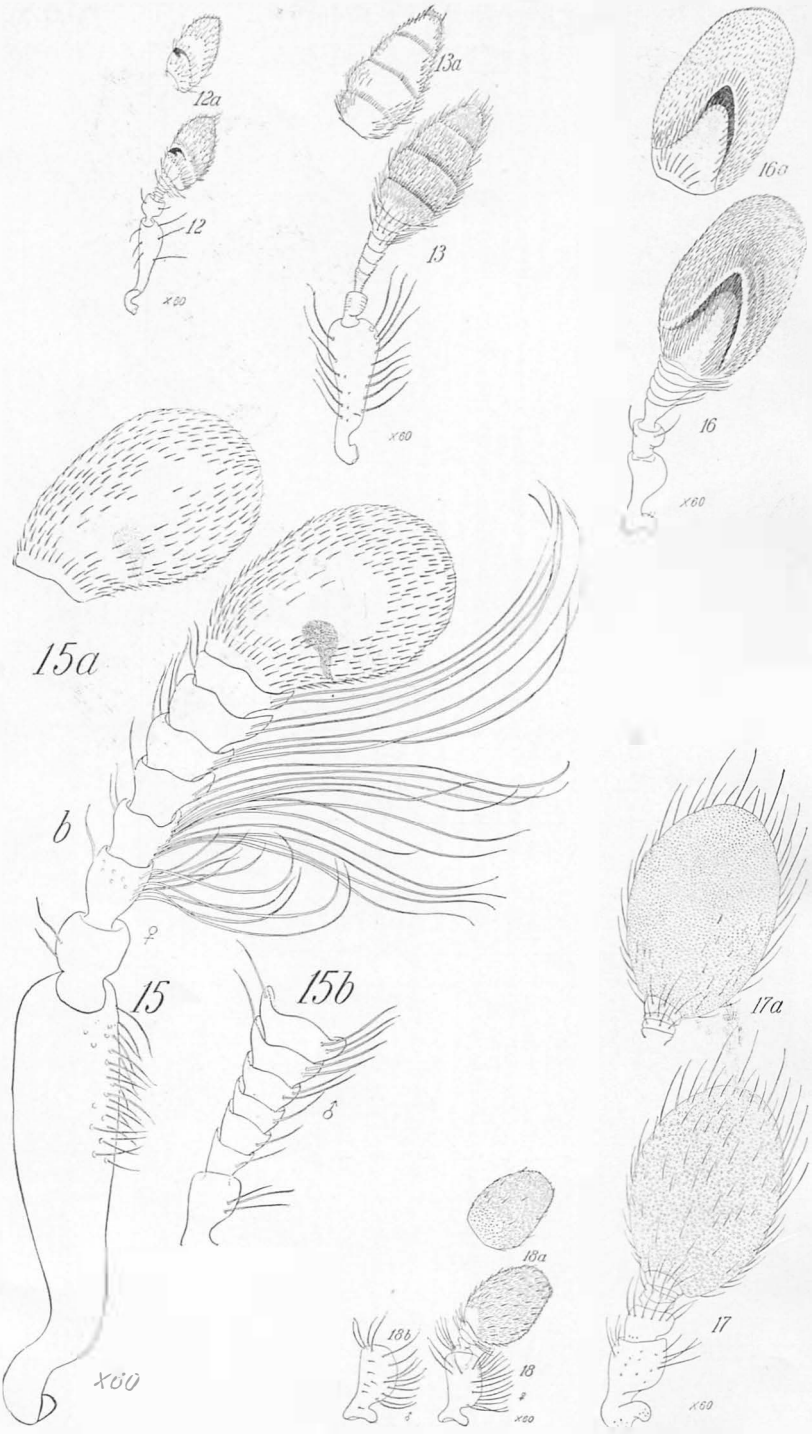
ANTENNÆ OF TYPICAL SPECIES OF THE SUBFAMILIES OF SCOLYTOIDEA.

Fig. 1.—*Cryphalus asperatus* (Cryphalinæ), anterior aspect of left antenna. Fig. 1*a*.—Posterior aspect of left antenna of same. Fig. 2.—*Ips typographus* (Ipinæ), anterior aspect of left antenna. Fig. 2*a*.—Posterior aspect of left antenna of same. Fig. 3.—*Corthylus columbianus* (Corthylinæ), female, anterior aspect of left antenna. Fig. 3*a*.—Female of same, posterior aspect of left antenna. Fig. 3*b*.—Male of same, club. Fig. 4.—*Micracis suturalis* (Micracinæ), female, anterior aspect of left antenna. Fig. 4*a*.—Female of same, posterior aspect of left antenna. Fig. 4*b*.—Male of same, scape. Fig. 5.—*Webbia dipterocarpi* (Webbinæ), anterior aspect of left antenna. Fig. 5*a*.—Posterior aspect of left antenna of same. (Original.)



ANTENNÆ OF TYPICAL SPECIES OF THE SUBFAMILIES OF SCOLYTOIDEA.

Fig. 7.—*Crypturgus pusillus* (Crypturginæ), anterior aspect of left antenna. Fig. 7*a*.—Posterior aspect of left antenna of same. Fig. 8.—*Phlœotribus oleæ* (Phlœotribinæ), anterior aspect of left antenna. Fig. 8*a*.—Posterior aspect of left antenna of same. Fig. 9.—*Hylesinus crenatus* (Hylesininæ), anterior aspect of left antenna. Fig. 9*a*.—Posterior aspect of left antenna of same. Fig. 10.—*Phlœoborus rudis* (Phlœoborinæ), anterior aspect of left antenna. Fig. 10*a*.—Posterior aspect of left antenna of same. (Original.)



ANTENNÆ OF TYPICAL GENERA OF THE SUBFAMILIES OF SCOLYTOIDEA.

Fig. 12.—*Hexacolus* sp. (Hexacolinæ), anterior aspect of left antenna. Fig. 12*a*.—Posterior aspect of left antenna of same. Fig. 13.—*Bothrosternus sculpturatus* (Bothrosterninæ), anterior aspect of left antenna. Fig. 13*a*.—Posterior aspect of left antenna of same. Fig. 15.—*Camptocerus æneipennis* (Camptocerinæ), anterior aspect of left antenna of female. Fig. 15*a*.—Club of female of same. Fig. 15*b*.—Scape of male of same. Fig. 16.—*Scolytus scolytus* (Scolytinæ), anterior aspect of left antenna. Fig. 16*a*.—Posterior aspect of left antenna of same. Fig. 17.—*Scolytoplatypus* sp. (Scolytoplatypodinæ), anterior aspect of left antenna. Fig. 17*a*.—Posterior aspect of left antenna of same. Fig. 18.—*Platypus cylindrus* (Platypodinæ), anterior aspect of left antenna of female. Fig. 18*a*.—Posterior aspect of left antenna of same. Fig. 18*b*.—Male scape of same. (Original.)

antennæ (145); eyes (143), epistoma (6), front of head (2)—total for head including antennæ (297); pronotum (29), elytra (12), tarsi (8), tibia (6), form of body (5), pygidium (2), abdominal sternites (2), and coxæ (5). Thus it is shown that the most important generic characters are found in the antennæ and eyes.

A summary of the principal character-bearing parts, as recognized by the writer in his preliminary classification, may be tabulated as follows:

TABLE I.—*Summary of principal character-bearing parts in the superfamily Scolytoidea.*

Characters.	In the superfamily.	In the families.	In the subfamilies.	In the subsections and series to the genera.
	Timesused.	*Timesused.*	*Timesused.*	*Timesused.*
Tarsi, first joint	2		7	
Tibia, apical angles	3		1	6
Head		8	35	237
Pronotum		10	5	29
Elytra		2	4	12
Third tarsal joint		4	7	8
Coxæ			3	5
Seventh abdominal sternite		2	3	2
Pygidium			2	

GENERIC CHARACTERS.

THE ANTENNÆ.

(Fig. 96; Pls. X–XII.)

ANTENNAL FUNICLE.

The antennal funicle is perhaps the most important taxonomic element of the scolytoid beetles. It is one of the first things to be looked for as a guide to the combination of characters which distinguish the genus and, at the same time, indicate its position in the classification. While the same number of joints may be paralleled many times in the genera of the same subfamily and in different subfamilies, the writer holds that, with very few exceptions, there must be the same number of joints in the funicle of all of the species of a genus. The exceptions are found in *Hypothenemus* and *Stephanoderes*, in which the males are smaller than the females and the antennal funicle has a less number of joints. The males in *Xyleborus* and allied genera are also smaller than the females, but usually have the same number of joints. Occasionally there is a smaller number or other abnormal developments. (See fig. 97.)

The writer's conclusions are based on the study of balsam mounts of representatives of all of the genera which have been available to him, and of a large percentage of the commoner species. It has been found that a normal variation in the number of joints in the

same sex of the species of a well-defined genus is exceedingly rare. Therefore, an odd number of joints in examples of the dominating sex either indicates an abnormal development or a different genus. If abnormalities occur, they may be easily detected by the combination of other generic characters. The number of joints in the antennal funicle of the scolytoid beetles is limited to seven, and there is probably no normal exception to this in the superfamily, and probably not in the entire Rhynchophora, or, if so, it will be exceedingly rare.

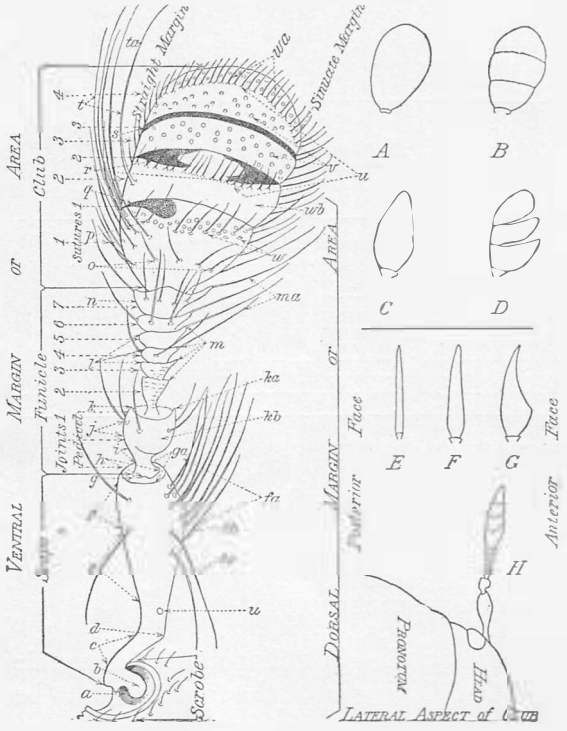


FIG. 96.—The antenna in scolytoid beetles: Diagram and terminology. *Scrobe:* *a*, Fossa. *Scape:* *b*, Condyle; *c*, basal section or neck; *d*, elbow; *e*, median section; *f*, apical section; *fa*, dorsal fringe; *g*, apical fossa; *ga*, apical margin. *Funicle:* *h*, Base or condyle; *i*, basal section; *j*, median section; *k*, apical section; *ka*, apical angle; *kb*, dorsal lobe; *l*, ventral angles of joints; *m*, dorsal angles; *ma*, funicular fringe or dorsal bristles; *n*, apical joint. *Club:* *o*, Basal annulation; *p*, apical or sutural annulation of joint 1; *q*, ventral septum or single septum; *r*, dorsal and ventral septa or double septa; *s*, chitinous suture; *t*, ventral fringe; *ta*, ventral bristle; *tb*, procumbent bristle; *tc*, recumbent bristle; *u*, setaceous annulation or sutural annulation; *v*, sensitive pores; *w*, sensitive and setal granules; *wa*, sensitive area; *wb*, chitinous area. *Club:* *A*, solid; *B*, annulated; *C*, conical; *D*, separated joints or sublamellate; *E*, compressed; *F*, thickened at base; *G*, obliquely truncate; *H*, antenna extending at right angles to the head. (Original.)

According to the number of joints in the funicle, the 221 genera, including many new ones, are distributed as follows:

TABLE II.—*Funicular joints in the superfamily Scolytoidea.*[a]

1 joint in 3 genera representing 1 subfamily.

2 joints in 6 genera representing 2 subfamilies.

3 joints in 13 genera representing 4 subfamilies.

4 joints in 44 genera representing 7 subfamilies.

5 joints in 73 genera representing 9 subfamilies.

6 joints in 31 genera representing 9 subfamilies.

7 joints in 51 genera representing 9 subfamilies.

Total, 221 genera representing 16 subfamilies.

Among eight genera of doubtful position the number of joints in the funicle is not given in the description of one genus. Three genera have 5, one has 6, and three have 7 joints.

Within the subfamilies the progressive modification in generic characters and characteristics appears to be associated with the

[a] This table includes eleven recently described genera which have been provisionally referred to subfamilies.

increase in the number of joints in the funicle. The exception to this rule appears to be shown in the Corthylinæ where the one-jointed and two-jointed funicles are characteristic of genera which, in certain lines, have progressed further than genera in other subfamilies with five, six, and seven joints. But it is by no means certain that these Corthylinæ are not highly specialized survivors of one of the most ancient groups in which a one-jointed funicle became the fixed and dominant character.

It is interesting to note in Table II that the five-jointed funicle is common to the greater number of genera. All but two of the classified genera with a five-jointed funicle fall in the subfamilies of the Ipidæ and the large majority of them in the first division; while the genera with a seven-jointed funicle fall in the last part of Division II of the Ipidæ and in the family Scolytidæ.

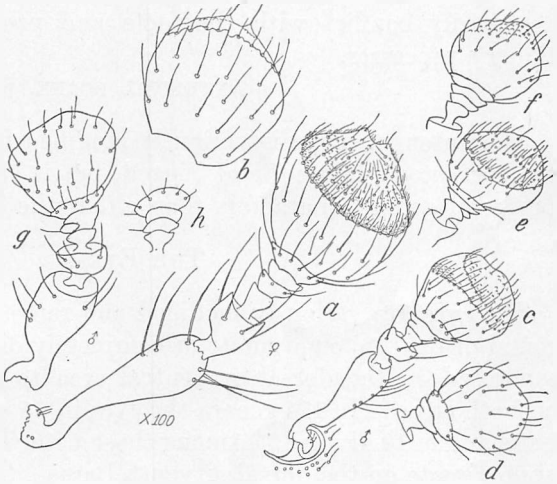


FIG. 97.—Abnormalities in the antennal funicle of *Xyleborus tachygraphus:* *a*, Anterior aspect of right antenna of female; *b*, posterior aspect of club of *a;* *c*, anterior aspect of left antenna of male; *d*, posterior aspect of club and funicle of *c;* *e*, anterior aspect of right club and funicle of same specimen as *c;* *f*, posterior aspect of *e;* *g*, posterior aspect of right antenna of another specimen; *h*, anterior aspect of *g*. (Original.)

ANTENNAL CLUB.

The antennal club comes next to the funicle as a bearer of important generic characters. The range in modifications of form is from a narrow, somewhat compressed and distinctly annulated club like that of *Hypothenemus* and *Pityophthorus* to the broad, thinly compressed, thickened at base, obliquely truncated, solid conical, or separated joint form.

In 179 genera 123 have a more or less compressed and annulated club, in 44 the club is thickened at base, and in 12 it is conical. In 170 genera 144 are annulated, 36 not annulated, and in 9 the joints are separated. In 136 genera 52 have sutural septa, 74 are without sutural septa, and 10 have chitinized sutures.

It appears that the chitinized septum of the club, while variable and paralleled in different genera, is a good generic character. The septa vary in number from one to four and usually occur toward the ventral margin, but may also occur toward the dorsal margin of one or two sutures. The range of modification appears to be

from a club with one or more septa to an annulated club with chitinized sutures and without septa, to a solid club without annulations or septa, or to a conical club with chitinized joints.

The septum is evidently the remnant of the chitinized elements of a movable joint, indicating that the progressive modification of the antennæ toward the opposite extreme has been by the process of reduction or fusion of two or more joints, while the modification of the funicle has evidently been along the line of accession by division as is indicated in the funicle of the retrograde sexual forms (fig. 97) and in the nymphs of certain Hemiptéra and Isoptera.

Thus we have in a single organ evidence of progressive modification by reversed processes which is not unreasonable and does not necessarily conflict with the facts and principles of other evolutionary processes.

ANTENNAL SCAPE.

The antennal scape is variously modified from simple and slender to short, stout, dilated, and fringed, but is of less importance as the bearer of generic characters than either the funicle or the club.

The Eyes.

The eyes are variously modified and range from simple, elliptical, round or oval, to emarginate or completely divided and from widely separated on the dorsal or ventral area to approximate on one or on both areas. In 114 genera the eyes in 65 are simple, in 98 emarginate, and in 10 divided. Among those with simple eyes, 4 have them approximate on the dorsal or ventral areas.

The Mouthparts.

The characters of the mouthparts have been quite extensively used by systematists in the definition of genera, but while the writer recognizes that some excellent characters are to be found in the mouthparts, he is convinced that they are by no means essential for the definition or classification of the genera. The principal objection to their use, as every systematist has doubtless recognized, is that they are not available for interpretation without mutilating the specimen, which in the case of rare or unique specimens and those from other collections is out of the question. Another serious objection is in the fact that no two balsam mounts of a maxilla of the same species present the same contours and angles, and, therefore, these may appear to be quite different except, perhaps, in the number and relative lengths of the joints of the palpus.

EPISTOMA.

The epistoma in all of the species examined shows more or less important generic and specific characters. There is a wide range of modification, from a simple, transverse, chitinous piece with few or no epistomal bristles to the epistomal process of *Dendroctonus* and the exceedingly long epistomal horn of *Cactopinus*, or the flattened labral-like form in *Pycnarthrum*.

HYPOSTOMA.

The hypostoma is also quite variable and can be used to good advantage in the more detailed definition of a genus or larger group.

LABRUM.

The absence of a true labrum in the adult scolytoid beetle appears to be universal. It has been stated by Eichhoff that it was present in *Pycnarthrum*, but an examination of a balsam mount has convinced the writer that this is only a produced median area of the epistoma.

CHARACTERS IN GENERAL.

The Body.

The size, form, color, vestiture, sculpture, and armature of the body represent characters of more or less importance in indicating lines of progressive modification and as aids in generic and specific definition. The size ranges from 0.4 or 0.5 mm. in the males of some *Hypothenemus* to 13 mm. in *Phlœoborus*. While there is more or less variation in the size of the individuals of a species, the length is important not only as a guide to the recognition of a species but as an index to its proper position in the minor section of the genus to which it belongs. The writer has found that, as a rule, the smaller species of a division, subdivision, or section of a genus will, according to other correlated characters, occupy a position opposite to that of the larger species. In the system adopted by the writer the genera with the average smaller species come first in the subfamily and in each primary and minor division, and in the genus the smaller forms, as a rule, precede the larger. There are, of course, exceptions to this rule, especially in genera with few and widely separated species.

FORM.

The form of the body ranges from elongate and slender to short and stout, and it would appear that the range in progressive modification is from the slender to the stouter forms.

COLOR.

The color, except in a few genera, is of little taxonomic importance. It ranges from pale yellow through yellowish red, reddish brown, brown, and black. In a few genera the chitinous integument of the elytra or other parts of the body is bicolored; in others the variegated color is confined to the vestiture. Metallic and iridescent colors are rare.

VESTITURE.

The vestiture is of considerable taxonomic importance. It consists of scales, stout hairs, barbed hairs, plain hairs, fine pubescence, gummy exudations, or adherents. The range in progressive modification of the vestiture appears to be from scales to stout hairs, from barbed hairs to simple hairs, and from a sparsely pubescent to an entirely glabrous body.

SCULPTURE.

In the sculpture of the body there is endless variety. It may be rugose or smooth, the rugosity fine or coarse, the punctures sparse or dense, arranged in rows or confused, regular or irregular in size, irregularly distributed on given areas, etc. Some of the elements of sculpture, such as the rugose or smooth pronotum, are of value in separating the major and minor groups of the families, but the characters of the rugosities and punctures are of special value in defining the smaller groups and species. Concavities and convexities of the front of the head and of the apical declivity of the elytra are often important generic, specific, and secondary sexual characters.

ARMATURES.

The armatures of the pronotum, head, and elytra are important in the definition of genera, species, and sexes. The armature of the head reaches its extreme development in the epistomal horn of *Cactopinus*. The armature of the declivity is strongly developed in *Xyleborus*, *Xylocleptes*, and *Eccoptopterus* of the Cryphalinæ; in *Pityogenes* and *Ips* of the Ipinæ; in *Hylocurus* in the Micracinæ; in *Monarthrum* and *Amphicranus* of the Corthylinæ, and in most of the genera of the Platypodinæ. As a rule the modification from a simple unarmed body to one with moderately or strongly armed parts is correlated with other elements of progressive modification. The serrate armature of the anterior margin of the pronotum is of considerable taxonomic importance. The apical serrations are common in the Cryphalinæ and Ipinæ, but rare or absent in the other subfamilies. The extremes in apical armature are found in *Hypothenemus miles* Lec., and in some other species, as, for example, the

males of certain species of *Xyleborus*, and in *Amphicranus fastigatus* Blndfd. The modification of the apex appears to progress from an apically serrate to a simple one or to one with an apical process.

HEAD.

The head is the most important part of the body in representing the greatest number of taxonomic characters. Its modification is from a short and narrow or broad and globular form concealed from above by the pronotum, toward a narrow elongate form exposed beyond the apical margin of the pronotum. The tendency toward the prolonged subrostrate form indicates a line of progressive modification which is characteristic of the major and minor groups of all of the Rhynchophora, the extremes of which are found in the small, short, globular head of the Ipidæ and the exceedingly prolonged beak of *Apion*, *Balaninus*, and other genera. In the Scolytoidea, *Cosmoderes* to *Stephanoderes* of the Cryphalinæ have the shortest, simplest head, while the extreme is reached in certain genera of the Hylesininæ, Hexacolinæ, and Chapuisinæ, with the extreme, or nearest approach to Curculionidæ, in *Hylurgops* and *Hylastes*. With a few exceptions the concealed head is characteristic of the first division of the Ipidæ and the Scolytidæ, while the exposed head is characteristic of the second division of the Ipidæ and the Platypodidæ. The antennæ, eyes, and mouthparts have been discussed in preceding pages. The front of the head is of special importance in defining the species and sexes, and ranges from convex and glabrous to deeply concave and densely pubescent.

PROTHORAX.

The prothorax (Part I, figs. 16 and 17, pp. 23–24) represents a wide range of progressive modification from long and narrow to short and broad; the pronotum with sides and base not margined to margined and simple or to emarginate, while the anterior dorsal area ranges from closely and finely rugose to coarsely asperate, and from alutaceous or opaque to smooth and shining. The pleura range from convex to flat and concave, the anterior coxæ from contiguous to widely separated, and the sternal, sternellar, and poststernellar areas vary with the form of the prothorax and the size and position of the coxæ. The vestiture and sculpture of the anterior median and posterior dorsal and lateral areas often represent generic and specific characters of special importance.

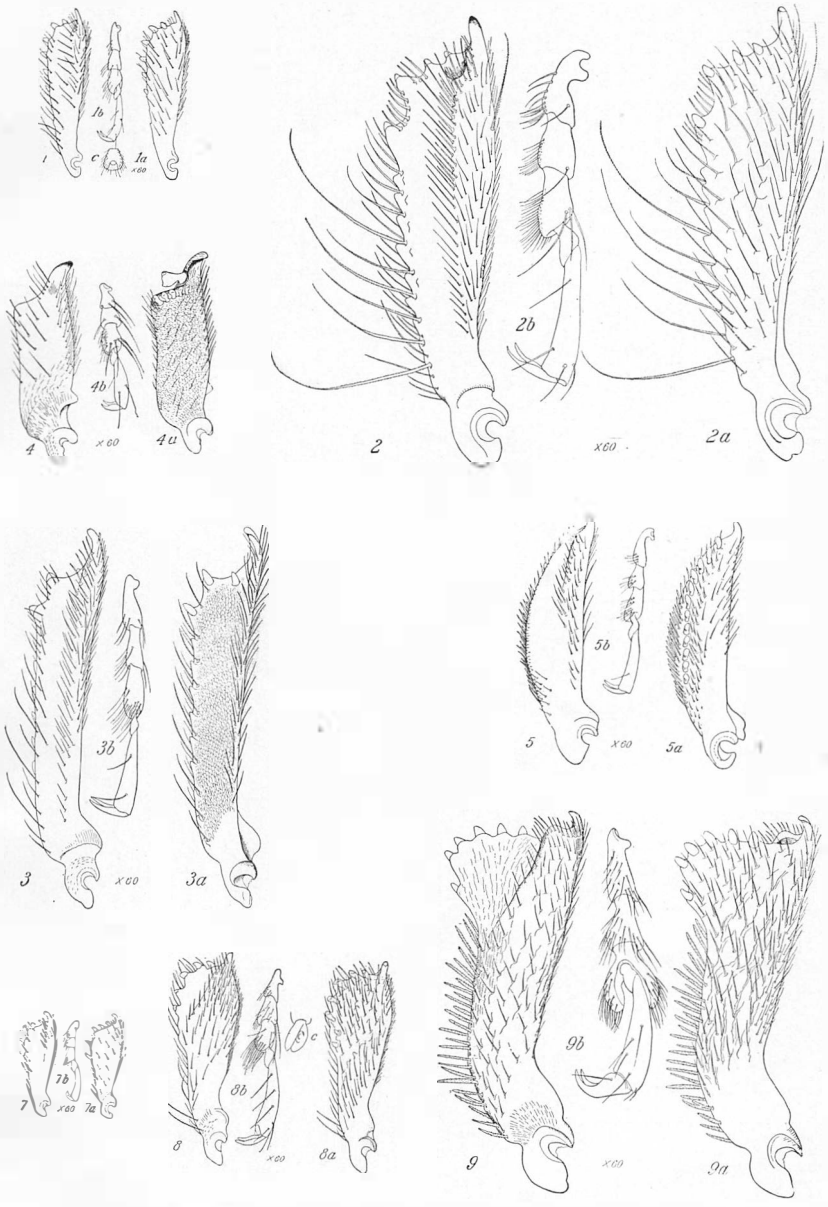
MESOTHORAX.

The mesothorax (Part I, figs. 18, 19) is exceedingly variable, conforming to the variable form of the body. It doubtless contains many group, generic, and specific characters which may settle difficult

questions of distinction and definition and should be considered in all detailed studies of single genera and allied groups of genera. The scutellum has been extensively used by systematists, and a detailed comparative study of this element in a wide range of genera and species should be made to determine its real significance in taxonomy. The pleurum (Part I, fig. 19) is also exceedingly variable in the form and sculpture of the epimeron, episternum, and preepisternum, while the remarkable structure designated as the preepisternal process (Part I, p. 29) is of special taxonomic importance since its presence or absence is peculiar not only to groups and divisions of the Scolytoidea but to many other groups of Coleoptera, and evidently represents an extreme in progressive modification which, in connection with other progressively modified elements, will doubtless serve as an index to the systematic position of genera and species. The elements of the sterna (Part I, fig. 18) are also variable, but, like the prosterna, their modification conforms to the variable form of the body, and they are of less importance than the more independent structures like the scutellum and preepisternal process.

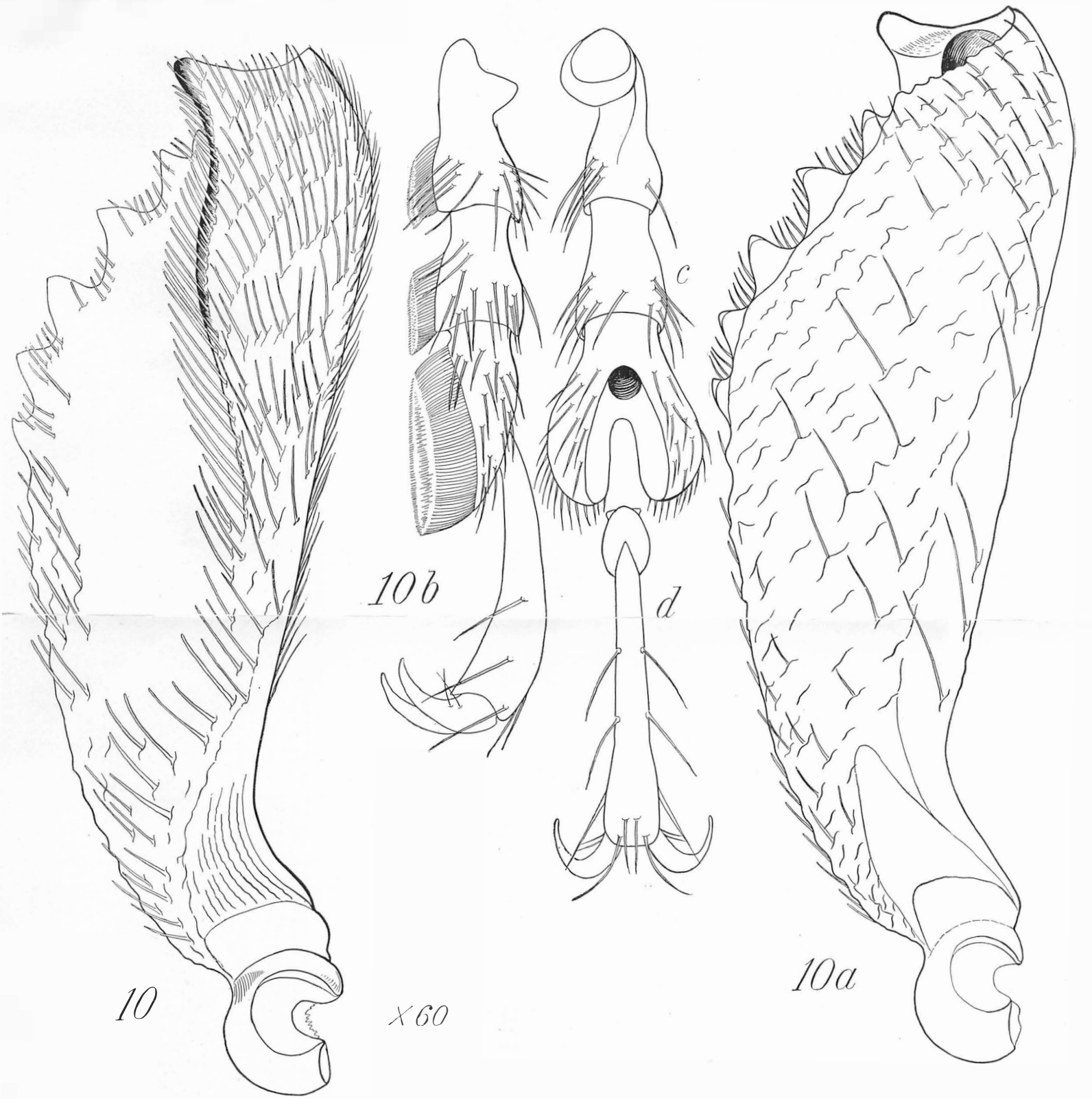
METATHORAX.

The metathorax (Part I, figs. 20, 21) is quite variable in general characters and especially so in some of the elements of the tergum, probably due to the variable form of the body and the requirements of flight. There is considerable variation of this element within the species of a genus and often there are wide differences in allied genera. Perhaps the element subject to the greatest variation is the postscutellum, which ranges from obscure or rudimentary to almost the length of the combined anterior elements. The scutellar groove, the transverse sutures, and the entothoracic ridges or apodemes are also quite variable. The writer has examined the metatergum of quite a large number of species and it would appear that there may be in it some important characters peculiar to minor groups of genera, but the taxonomic value of the variations is largely limited to the species. It would therefore be difficult to trace correlated lines of progressive modification. Nevertheless, a special comparative study of the metathorax should be made of a very large number of examples representing all of the genera to determine whether or not there are special taxonomic elements or recognizable lines of modification. The episternum (Part I, fig. 20) is quite variable in length, width, sculpture, and vestiture and is of considerable taxonomic importance. The metasterna are also variable in conformity with the variable form of the body. The sternum always occupies the greater part or nearly all of the area. The greatest range of variation between the elements of the metathorax is to be found in the short and broad forms of the stouter species of the Ipidæ and Scolytidæ and the exceedingly long and narrow forms peculiar to the Platypodidæ.



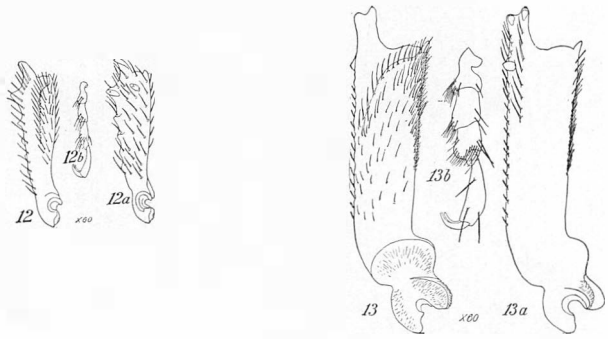
TIBIÆ AND TARSI OF TYPICAL SPECIES OF THE SUBFAMILIES OF SCOLYTOIDEA.

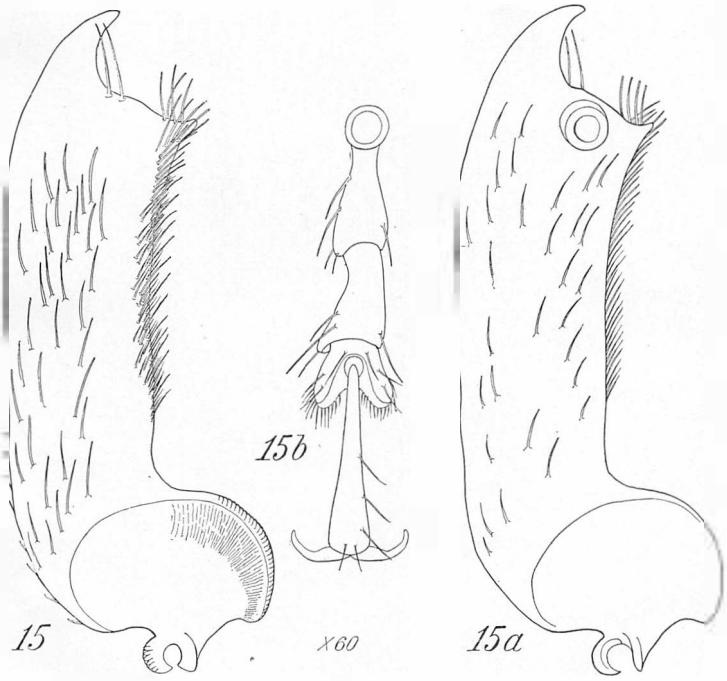
Fig. 1.—*Cryphalus asperatus* (Cryphalinæ), left tibia, dorsal aspect. Fig. 1*a*.—Left tibia of same, ventral aspect. Fig. 1*b*.—Tarsus of same, lateral aspect; *c*, third tarsal joint, dorsal aspect. Fig. 2.—*Ips typographus* (Ipinæ), left tibia, dorsal aspect. Fig. 2*a*.—Left tibia of same, ventral aspect. Fig. 2*b*.—Left tarsus of same, lateral aspect. Fig. 3.—*Corthylus columbianus* (Corthylinæ), left tibia of same, dorsal aspect. Fig. 3*a*.—Left tibia of same, ventral aspect. Fig. 3*b*.—Left tarsus of same, lateral aspect. Fig. 4.—*Micracis suturalis* (Micracinæ), left tibia, dorsal aspect. Fig. 4*a*.—Left tibia of same, ventral aspect. Fig. 4*b*.—Left tarsus of same, lateral aspect. Fig. 5.—*Webbia dipterocarpi* (Webbinæ), left tibia, dorsal aspect. Fig. 5*a*.—Left tibia of same, ventral aspect. Fig. 5*b*.—Left tarsus of same, lateral aspect. Fig. 7.—*Crypturgus pusillus* (Crypturginæ), left tibia, dorsal aspect. Fig. 7*a*.—Left tibia of same, ventral aspect. Fig. 7*b*.—Left tarsus of same, lateral aspect. Fig. 8.—*Phlœotribus oleæ* (Phlœotribinæ), left tibia, dorsal aspect. Fig. 8*a*.—Left tibia of same, ventral aspect. Fig. 8*b*.—Left tarsus of same, lateral aspect; *c*, third tarsal joint of same, subdorsal aspect. Fig. 9.—*Hylesinus venatus* (Hylesininæ), left tibia, dorsal aspect. Fig. 9*a*.—Left tibia of same, ventral aspect. Fig. 9*b*.—Tarsus of same, sublateral aspect. (Original.)



TIBIÆ AND TARSI OF TYPICAL SPECIES OF THE SUBFAMILIES OF SCOLYTOIDEA.

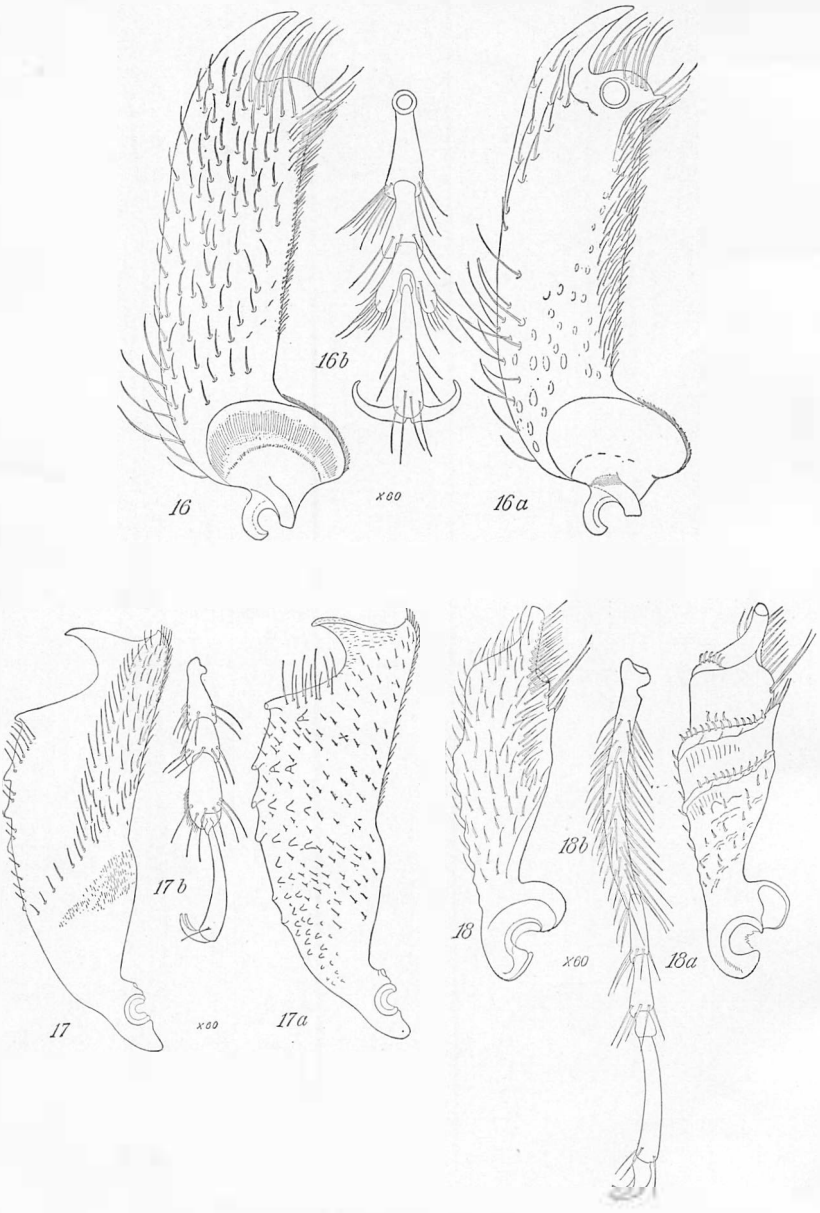
Fig. 10.—*Phlœoborus rudis* (Phlœoborinæ), left tibia, dorsal aspect. Fig. 10*a*.—Left tibia, ventral aspect. Fig. 10*b*.—Left tarsus of same, lateral aspect; *c*, left tarsus, dorsal aspect of joints 1-3; *d*, left tarsus, dorsal aspect of joints 4-5. (Original.)





TIBIÆ AND TARSI OF TYPICAL SPECIES OF THE SUBFAMILIES OF SCOLYTOIDEA.

Fig. 12.—*Hexacolus* sp., left tibia, dorsal aspect. Fig. 12*a*.—Left tibia of same, ventral aspect. Fig. 12*b*.—Left tibia of same, lateral aspect. Fig. 13.—*Bothrosternus sculpturatus* (Bothrosterninæ), left tibia, dorsal aspect. Fig. 13*a*.—Left tibia of same, ventral aspect. Fig. 13*b*.—Left tarsus of same, lateral aspect. Fig. 15.—*Camptocerus æneipennis* (Camptocerinæ), left tibia, dorsal aspect. Fig. 15*a*.—Left tibia of same, ventral aspect. Fig. 15*b*.—Left tarsus of same, dorsal aspect. (Original.)



TIBIÆ AND TARSI OF TYPICAL SPECIES OF THE SUBFAMILIES OF SCOLYTOIDEA.

Fig. 16.—*Scolytus scolytus* (Scolytinæ), left tibia, dorsal aspect. Fig. 16*a*.—Left tibia of same, ventral aspect. Fig. 16*b*.—Left tarsus of same, dorsal aspect. Fig. 17.—*Scolytoplatypus* sp. (Scolytoplatypodinæ), left tibia, dorsal aspect. Fig. 17*a*.—Left tibia of same, ventral aspect. Fig. 17*b*.—Left tarsus of same, dorsal aspect. Fig. 18.—*Platypus cylindrus* (Platypodinæ), left tibia, dorsal aspect. Fig. 18*a*.—Left tibia of same, ventral aspect. Fig. 18*b*.—Left tarsus of same, lateral aspect. (Original.)

LEGS.

There is a wide range of variation in the form, color, sculpture, and relative proportions of the coxa, trochanter, tibia, and tarsus of the anterior, median, and posterior legs. (Part I, figs. 1, 3, 26–29.)[a] The anterior tibia and tarsus are of special taxonomic importance in distinguishing the primary and secondary divisions of the superfamily and, to a less extent, in distinguishing the primary or minor groups of the families, subfamilies, and genera. (Pls. X, XIII–XVI.) The variation in the tibia is from a simple, compressed, slightly dilated form with the outer margin serrate, as in *Hypothenemus*, to a short, broad form with parallel, smooth margins, as in *Micracis* and *Scolytus*, or broader at the base, as in *Webbia* and *Hypoborus*, and to extreme and odd forms as in *Platypus*. The character of the vestiture usually conforms to that of the body, such as scales, barbed hairs, and simple hairs, varying in distribution and density on the ventral and dorsal areas and the margins. The sculpture ranges from smooth to imbricate and from irregular rugosities to prominent ridges, the latter reaching a maximum development in Platypodidæ. The tarsi vary in form from slender to stout and the joints in relative lengths, widths, and vestiture. The third joint varies from simple to emarginate and deeply bilobed, with the ventral surface ranging from nearly glabrous to pubescent and to densely padded, which latter extreme is found in *Phlœoborus*.

ELYTRA.

The elytra, or anterior wings, are exceedingly variable in form, vestiture, and sculpture, ranging from the simple types with scales, fine punctures, and obscure striæ which are not impressed, as in *Hypothenemus*, to the forms with hairs and with distinctly impressed striæ and elevated interspaces, the latter with rugosities and rows of punctures or smooth and without punctures; the base from plain to strongly elevated and serrate; the sides from parallel to converging posteriorly or strongly rounded; the dorsal area from flat and straight to convex and strongly rounded from base to apex; the declivity from plain, steep, and convex to retuse or armed and strongly oblique from base to apex, and the side margins from serrate to straight or emarginate. With all of these almost endless variations and their different combinations of elements there is available a profusion of characters for the definition of groups of genera and species.

POSTERIOR WINGS.

The true functional wings, as pointed out by Nüsslin (1911), are quite variable in form, proportions, and character of the venation and represent two specified types, one with and the other without

[a] Figures 26–29, Part I, represent the reverse faces of the *right* instead of the *left* tibia, a mistake which was unfortunately overlooked in the manuscript and proofs.

a basal lobe. The writer has given considerable attention to the study of the wings of the Scolytoidea and other insects, but he has failed to find any constant and readily recognizable characters in the Scolytoidea which appear to be of sufficient taxonomic value to justify giving them special attention. If there is any particular line of progressive modification in the wings it is to be found in the subfamilies and minor groups, in which the range appears to be from a simple type, like that of *Hypothenemus*, *Cryphalus*, and *Crypturgus*, with a narrow, simple base, long fringe, and simple venation, toward a broader base, lobed or not, and with an increasing number and complexity of veins. The writer realizes that the complex type of venation is generally supposed to be more primitive than the simple type with few or no veins, but he is by no means convinced that this is the correct interpretation as applied to the wings of all insects. The wings in different orders of insects may be, in spite of the prevailing opinion, the result of independent origin from simple types of primitive winglike processes, and their evolution may have been influenced by two primary factors: (1) A dominant tendency to perpetuate and promote lines of modification peculiar to and in conformity with the dominant morphological characters peculiar to the order, and (2) adjustment of this modification to the peculiar mechanical needs of the varying related forms, with frequent examples of parallel modifications in unrelated species.

In Nüsslin's table (1911, pp. 302–304) the wings without basal lobes are found in widely separated genera, representing, according to the present writer's classification, two families (Ipidæ and Scolytidæ) and five subfamilies, while the wings with basal lobes are found in five subfamilies of the Ipidæ. It is evident that whenever the wings are studied in their relation to other of the more important taxonomic characters and characteristics of the species, the variations noted by Nüsslin will be of considerable value in the definition of minor groups of genera and species, but the difficulty of spreading the wings and securing good balsam mounts will preclude their general use.

ABDOMINAL TERGITES.

The general character of the abdominal tergites is shown in Part I, figures 22, 23, and 24. While there is considerable variation in the first to sixth tergites, inclusive, in the same individual and between individuals of different species, the seventh and eighth are the ones of special importance in the identification of the genus or sex. According to Nüsslin (1911), who examined 16 genera, the eighth tergite is not covered in either sex in 11 genera, and is exposed in the male and covered in the female in 5 genera. The writer has found

the eighth to be uncovered in both sexes in three genera, uncovered in the male and covered in the female in 13 genera, and covered in both sexes in 3 genera.

According to the writer's classification, the 31 genera in which species were examined by Nüsslin and the writer represent the following subfamilies:

TABLE III.—*Abdominal tergites in the subfamilies of Scolytoidea in which species were examined by Nüsslin and the writer.*

Subfamily.	Eighth tergite uncovered in both sexes.	Eighth tergite uncovered in male, not in female.	Eighth tergite covered in both sexes.
	Genera.	*Genera.*	*Genera.*
Cryphalinæ	6	3	
Ipinæ	2	2	
Corthylinæ		4	
Micracinæ	1	1	
Crypturginæ	2		
Phlœotribinæ		2	
Hylesininæ	1	4	
Scolytinæ		1	
Platypodinæ			3
Total	12	17	3

From the foregoing it will be seen that the characters of the seventh and eighth tergites are paralleled in widely separated genera and subfamilies. The writer has found that the eighth tergite may or may not be exposed or covered in the same genus or in individuals of the same species, especially in *Platypus*, where the eighth tergite is of the same or similar form in both sexes and may be covered or not, depending upon the expansion or contraction of the abdomen. It is evident that a much more extensive study of these elements is necessary before any conclusions are warranted as to their taxonomic value or lines of progressive modification. In a number of genera the seventh or eighth tergite, or both, is exposed beyond the apex of the elytra and is either oblique, declivous, or vertical. The ninth and tenth tergites are absent as such or are modified into elements of the genital organs.

ABDOMINAL SPIRACLES.

According to Nüsslin (1911) and Fuchs (1912) the number of functional abdominal spiracles (stigmata) ranges from five to seven. The larvæ and pupæ, so far as studied by the writer, have eight.

The spiracles are variable in structure and doubtless, upon further investigation, will furnish excellent taxonomic characters. The writer, however, is doubtful as to the phylogenetic significance of the variability in number. The genera given by Nüsslin (1911, pp. 2–5) and Fuchs (1912, pp. 13–14) which are represented by species having

from five to eight spiracles fall into the following subfamilies as recognized by the writer:

TABLE IV.—*Abdominal spiracles in the subfamilies of Scolytoidea in which species were examined by Nüsslin and Fuchs.*

Subfamily.	Eight spiracles.[a]	Seven spiracles.	Six spiracles.	Five spiracles.
	Genera.	*Genera.*	*Genera.*	*Genera.*
Cryphalinæ		2	3	2
Ipinæ		1		
Corthylinæ			1	
Micracinæ				2
Crypturginæ	1	2		1
Phlœotribinæ		1	1	4
Hylesininæ	1	3	2	3
Scolytinæ		1		
Total	2	15	7	12

[a] The eighth spiracle is rudimentary.

In the genus *Hylesinus* (Fuchs, ibid., p. 13) there are from five to seven spiracles with the sixth and seventh rudimentary, while in *Dendroctonus* and *Hylurgops* the eighth is rudimentary. Doubtless if the number of abdominal spiracles were determined for all of the species, some good evidence would be furnished as to lines of modification.

ABDOMINAL STERNITES.

The abdominal sternites 1 and 2 are fused and concealed in the coxal cavity, 3 to 7 are exposed, and the eighth is covered by the seventh, while the ninth and tenth evidently are represented by the genital organs. (See Pt. I, pp. 25 and 38, and Technical Series 20, Pt. I, Pls. VII, VIII, and IX, as also the discussion of the reproductive organs in the present paper.) The exposed sternites are quite variable in the different genera and species, and certain characters are of value in designating minor groups of genera, but few, if any, are common or peculiar to a subfamily.

The modifications range from the simple type found in the Cryphalinæ to the steep, excavated, armed, and odd forms of the Scolytidæ and Platypodidæ. There is a wide variation, which is apparently of specific importance, in the eighth ventral segment. The palpi of the ninth ventral segment (Nüsslin, Fuchs, and others) found in the females of *Scolytus* and *Hylesinus*, may after all represent the tenth tergite or sternite, one or both of which may be represented by the ovipositor as in certain Curculionoidea (*Pissodes*), Cerambycoidea (*Cyllene*), and many other insects. But this is a matter requiring more comprehensive investigation.

STRIDULATING ACCESSORIES.

The stridulating accessories have not been investigated by the writer in many genera but they appear to be confined largely to the seventh abdominal tergite and the inner subapical area of the elytra

(Part I, figs. 23, 31, and 33) and to the anterior margin of the pronotum and the posterior dorsal area of the head.

Internal Anatomy.

Considerable study has been made by Lindemann, Nüsslin, Fuchs, and others, of certain elements of the internal anatomy, especially the proventriculus of the digestive system and the male and female reproductive organs. It is evident, however, from a review of the

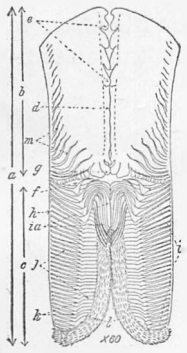


FIG. 98.—Proventricular plate of *Ips emarginatus*, inner aspect: *a*, Entire plate; *b*, divided anterior plate; *c*, posterior or masticatory plate; *d*, median longitudinal suture; *e*, sutural teeth; *f*, median transverse suture; *g*, transverse or apical teeth of anterior plate; *h*, lateral margin or marginal suture; *i*, lateral or masticatory teeth; *ia*, closing bristles or teeth; *j*, femora of the masticatory teeth; *k*, femoral teeth or ridge; *l*, masticatory brush; *m*, marginal bristles or fringe. (Original.)

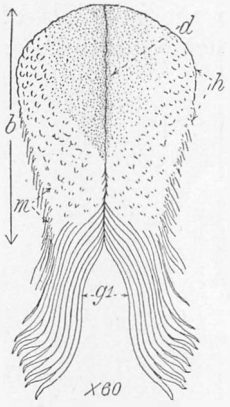


FIG. 99.—Proventricular plate of *Scolytus scolytus*: *b*, Divided anterior plate; *d*, mediansuture; *h*, lateral margin; *g1*, apical laminate teeth of posterior plate. (Original.)

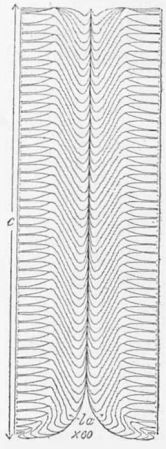


FIG. 100.—Masticatory plate of *Crossotarsus lecontei*: *c*, Masticatory plate; *la*, apex and lateral serrations of masticatory teeth. This figure should be viewed in a reversed position in order to recognize the elevated character of the median longitudinal area. (Original.)

results, that as a sufficient basis for general or specific conclusions a far more comprehensive study is necessary.

DIGESTIVE SYSTEM.

The general type of the digestive system is shown in Part I, figures 35 and 36, for the adult and figure 43 for the larva. Lindemann (1876, pp. 148–169), Nüsslin (1912, pp. 85–87, figs. 135–143), and Sedlaczek (1902, pp. 241–263, figs. 1–20) show that there is a wide variation in some of the elements and especially in the proventriculus and the median and posterior section of the midintestine, but to what extent these variations are of value in taxonomy has not been determined.

Proventriculus.

The proventriculus (figs. 98–100; Part I, figs. 35–38) is of special interest, and the work of Lindemann, Fuchs, Nüsslin, and others has contributed much valuable information on the structural elements.

There is a wide range of variation in the proventricular plates and their armatures, such as the various divided and undivided forms with and without the "brush" of fine masticatory teeth. These variable forms appear to be of considerable taxonomic importance when correlated with other internal and external characters.

The classification proposed by Lindemann and Nüsslin, as based on the structural characters of the proventricular plates, with a few plainly evident exceptions, correlates in a striking manner with the external characters adopted by the writer for the major and minor groups of genera. When the principle of parallel modification is considered, the genera which seem to be out of place in the classifi-

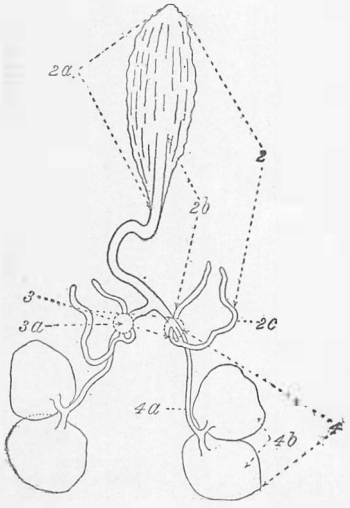


FIG. 101.—*Dendroctonus valens:* Membranous and nonchitinous elements of the male reproductive organs. See terminology under Divisions 2, 3, 4, pp. 192–193. (Original.)

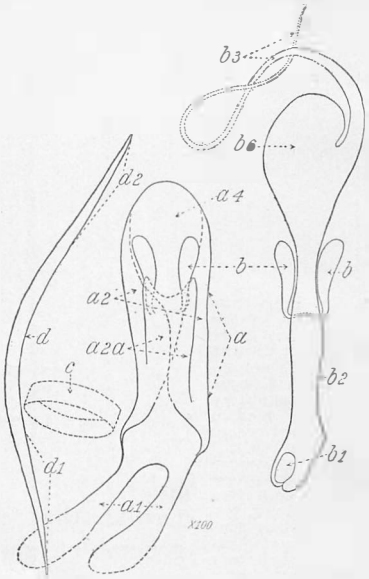


FIG. 102.—*Xyleborus saxeseni:* Chitinous elements of male reproductive organs. See terminology, Division 1, pp. 192–193. (Original.)

cations based on proventricular characters alone will, when correlated with a combination of characters, fall into their natural positions.

REPRODUCTIVE ORGANS.

THE REPRODUCTIVE ORGANS OF THE MALE.

The reproductive organs of the male (figs. 101–110) have been studied and figured by several investigators as follows:

TABLE V.—*Summary of previous studies of the male reproductive organs by various authors.*

Author.	Year of publication.	Number of species figured.	Number of genera represented.
Lindemann	1875	32	15
Verhoeff	1896	3	3
Fuchs	1911	20	4
Nüsslin	1912	24	22
Fuchs	1912	30	27
Sharp	1912	2	2

In addition to the foregoing, the writer, during the years from 1892 to 1912, has studied the male reproductive organs of 68 species, representing 43 genera. The total species studied by all authors, without duplication, is 147, representing 57 genera.

The reproductive organs of the male represent four primary divisions or elements: (1) The posterior chitinized division (fig. 102), (2) the posterior membranous division (fig. 101), (3) the median division, and (4) the anterior division. (See terminology, pp. 192–194.)

POSTERIOR ELEMENTS.

The posterior chitinized elements (division 1) consist of four primary sections, (*a*) the body, (*b*) the end plates, (*c*) the tegmen, and (*d*) the spicule. In addition to these more constant elements there are (*b1*) the seminal valve and (*b2*) the seminal rod, both of which appear to be more intimately associated with element *b* than with element *a*; also, there are (*e*) the connecting membrane and (*f*) the muscles. From a somewhat comprehensive study of the chitinized elements in the scolytoid beetles in comparison with those in other insects it seems plain that, so far as these beetles are concerned, the chitinized parts of the male reproductive organs represent elements of the ninth and tenth abdominal segments, either as direct modifications of primitive sclerites or as independent developments

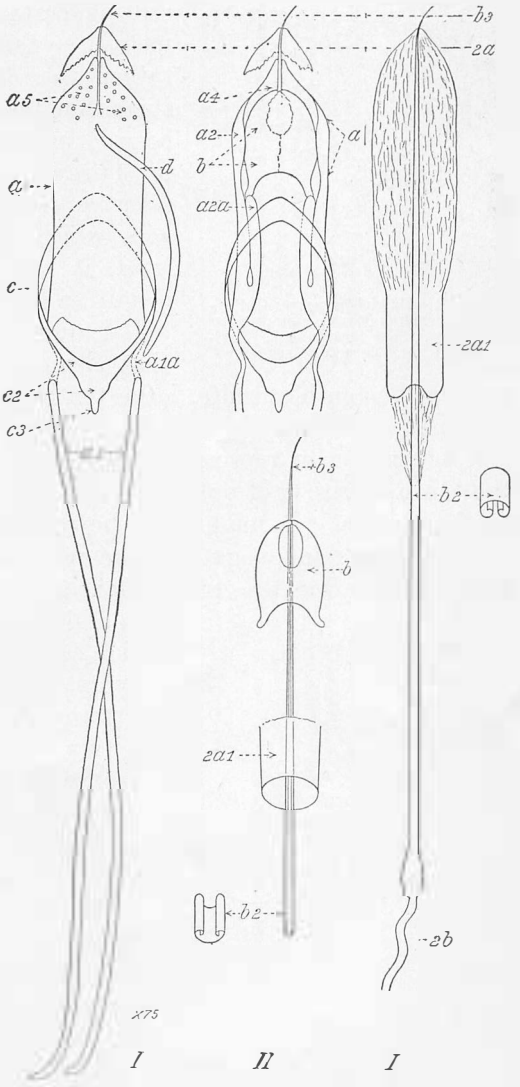


FIG. 103.—*Ips emarginatus:* Chitinous elements of male reproductive organs. *I*, ventral aspect; *II*, dorsal aspect. See terminology, Division 1, pp. 192–193. (Original.)

from the same fundamental source as that from which the various segmental lobes, sclerites, and appendages have developed. It would appear best to refer to the chitinous element of the copulatory apparatus as representing certain segmental elements rather than to assume that they have been derived through modification from sclerites or appendages which had existed as such in a primitive ancestor.

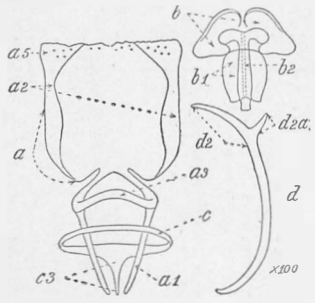


FIG. 104.—*Pityophthorus* sp.: Chitinous elements of male reproductive organs. See terminology, Division 1, pp. 192-193. (Original.)

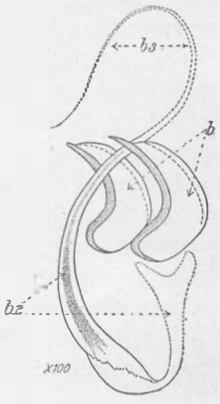


FIG. 105.—*Pityophthorus bellus:* End plates and seminal rod of male reproductive organs, lateral aspect. Note contrast between this and fig. 104. See terminology, Division 1, pp. 192-193. (Original.)

It is quite evident that element *a* represents the tenth sternite, *b* the tenth tergite, *c* the ninth tergite, and *d* the ninth sternite, while *b1* and *b2* appear to represent elements of either the tenth tergite or of both the tenth tergite and tenth sternite. It might also be well to consider in future investigations the possibility of their representing the tenth pleurites or even an additional eleventh segment. The wide range in the variation of these elements, the absence of some of them in certain species, and the joining or fusion of two or more in other species render it exceedingly difficult properly to interpret the primary and secondary elements, especially in the more complex and in the apparently simple forms.

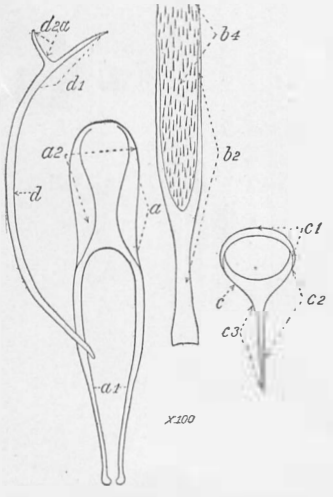


FIG. 106.—*Micracis suturalis:* Posterior elements of male reproductive organs, dorsal aspect. See terminology, Division 1, pp. 192-193. (Original.)

The body, or element *a*, is present in all species. It is more or less distinct from the other elements and is nearly always suggestive of a modified sternite; the femora (*a1*) appear to represent the produced posterior angles, or apodemes, of a typical abdominal sclerite, and the lateral folds (*a2*) appear in some cases to represent the hypopleurites, especially in *Ips*, where they resemble end plates and were so identified by Lindemann. The function of element *a* is that of a sheath or tube for the ejaculatory sack (*2a*) and for the seminal valve

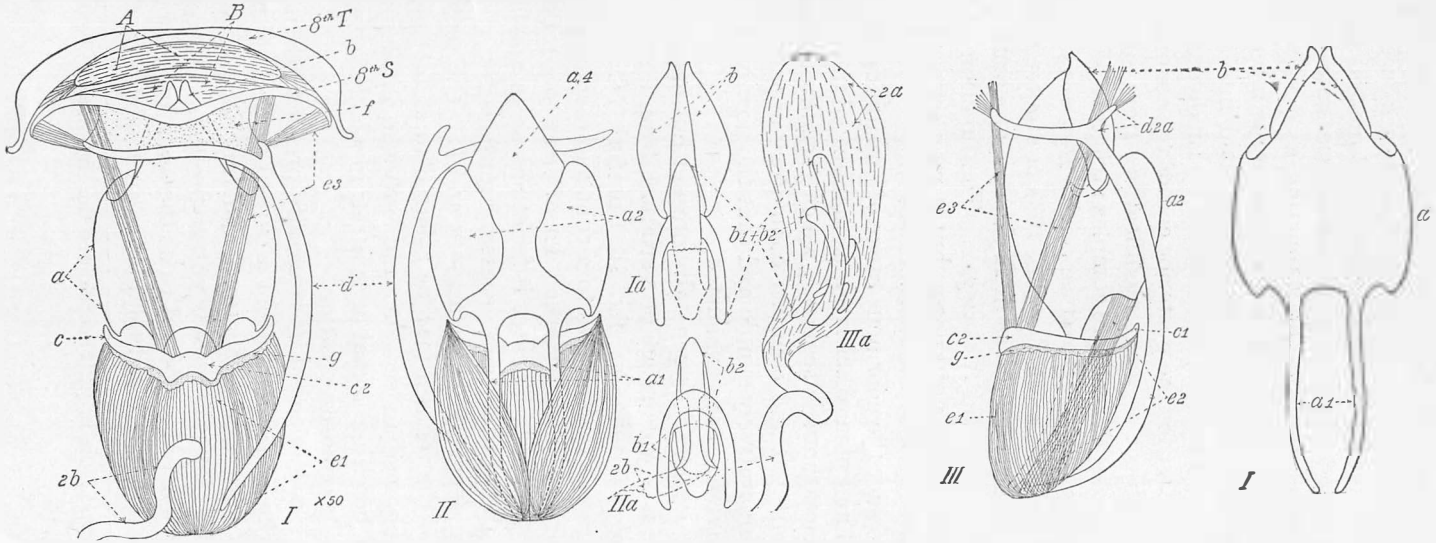


FIG. 107.—*Dendroctonus valens*: Posterior elements of male reproductive organs. *I*, ventral aspect; *II*, dorsal aspect; *III*, lateral aspect; *A*, anal orifice; *B*, genital orifice; *8th T*, eighth tergite; *8th S*, eighth sternite or genital plate; *Ia*, ventral aspect of seminal valve and accessories; *IIa*, dorsal aspect of same; *IIIa*, lateral aspect of same. See terminology, Division 1, pp. 192–193. (Original.)

(*b1*) or the seminal rod (*b2*), or both, as the case may be. The end plates (*b*) are commonly present. They are sometimes fused with *a2* but are more often separated or more directly connected with *b1* or *b2*.[a] The end plates proper appear to function as accessories to *a* in forming the sheath or outer tube; *b1* may function as a valve to close the seminal duct while muscular or blood pressure is brought to bear on the ejaculatory sack to force the seminal fluid into the copulatory pouch, or they may function, as indicated by Lindemann, as a furrow or troughlike support for the posterior end of the seminal duct. The end plates are subject to great modification, from simple chitinous pieces, as in *Pissodes*, to the more complex structure with many parts, as in *Dendroctonus* (fig. 107), and especially *Hylesinus*, or into a long slender troughlike rod, as in *Ips* (fig. 103), a stouter rod with apical dilation and a long flagellum, as in *Xyleborus*, or a brushlike form, as in *Micracis* (fig. 106), and *Xylocleptes*. The function of the slender rod or apical filament is not known, but it may serve to conduct the seminal fluid directly into the spermathecal duct.

When we consider the enormous range of possibilities in the modification of tergal and pleural sclerites, as manifested in the tergum and pleura of the metathoracic segment, we can readily understand that the most complicated and complex copulatory apparatus yet found in insects is comparatively simple and that the possibilities of further modification have not been exhausted.

The tegmen, or ring (*c*), is generally present but may be obscure or absent. There is a wide range of variation, from a simple and ventral plate (*Scolytus rugulosus*, fig. 108) or fork (*S. quadrispinosus*, fig. 109, and *Crossotarsus*, fig. 110) to a continuous simple ring or band (fig. 102), and from a plain or forked dorsal piece to a forked or plain ventral piece. In nearly all cases it functions as an apodeme for the attachment of the primary and accessory muscles for the posterior extension and movements of elements *a* and *b*. The sections of the various forms of the tegmen may be referred to as (*c1*) the posterior section, (*c2*) the median section, and (*c3*) the apodemal process. Section *c1* may be either dorsal or ventral; in whichever case section *c2* will occupy the opposite position.

The spicule or rod (element *d*) is usually present in a more or less distinct form which may vary from a curved forked rod to a simple rod, and in its various modifications and functions may occupy a dorsal, sublateral, lateral, or subventral position. The sections of the various forms may be referred to as the anterior section (*d1*) and the posterior section (*d2*). It functions as an apodeme for the attach-

[a] Verhoeff (1896) and Nüsslin (1912) considered the end plates as belonging to the body.

ment of the primary and accessory muscles for the retractile movements of the tube (*a* and *b*).

The muscles (*e*) are more or less complicated and variable in size, number, and attachments. In some cases, as in *Dendroctonus*, the

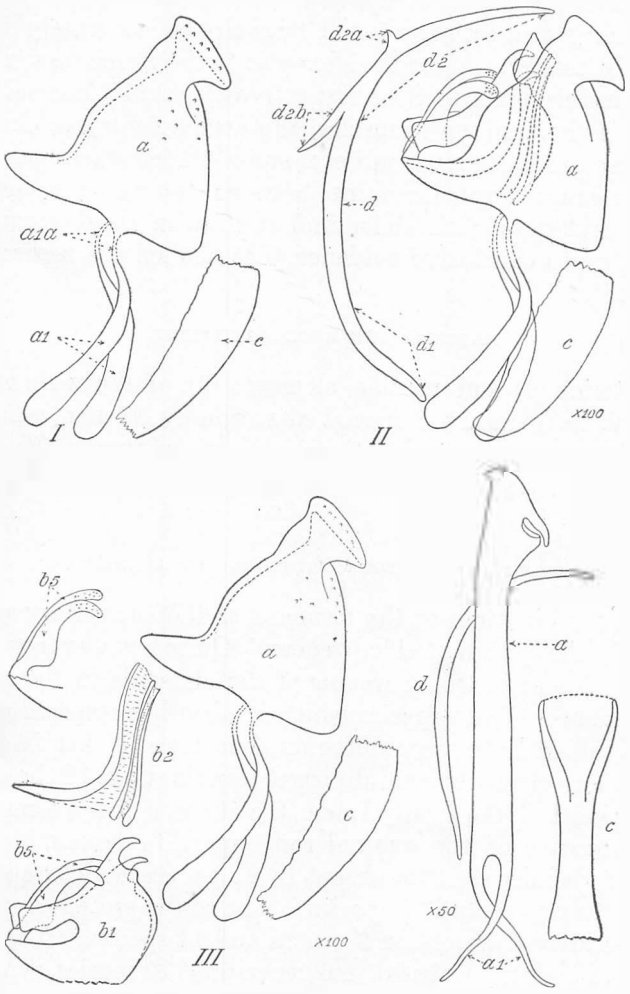


FIG. 108.—*Scolytus rugulosus:* Posterior elements of male reproductive organs. *I*, lateral aspect of body; *II*, lateral aspect of body and accessories in situ; *III*, body accessories separated. See terminology, Division 1, pp. 192–193. (Original.)

FIG. 109.—*Scolytus quadrispinosus:* Posterior elements of male reproductive organs, lateral aspect. See terminology, Division 1, pp. 192–193. (Original.)

extensor and retractile muscles are prominent, the former (*e1*) attached posteriorly to the anterior edge of element *c*, while the supplementary muscles (*e3*) are attached anteriorly to the posterior edge of *c* and posteriorly to the inner surface of the eighth sternite, as in *Dendroctonus*, or to the anterior section of element *c* and the eighth

tergite, as in *Crossotarsus*. In *Dendroctonus* the retractile muscles (*e2*) are attached to the anterior end of the spicule (*d*) and to the basal angles of the body (*a*), while in *Crossotarsus* they are attached to *e2* and to the sides of a ventral groove in *a*.

The connecting membrane (*f*) is very difficult to locate and follow to its primary connections, but if it could be accurately traced it would doubtless furnish good evidence as to the proper assignment of the chitinous elements to their respective tergal and sternal origins, unless, as is the case with muscles, the attachments are changed or even reversed to harmonize and economize the requirements of function. The connecting membrane between the posterior section of element *d* and the eighth abdominal sternite in *Dendroctonus* seems to furnish quite conclusive evidence that the spicule represents the ninth sternite.

ANTERIOR AND MEDIAN ELEMENTS.

The anterior (4) and median elements (3) of the male reproductive organs have received special attention by Nüsslin, who bases a classification on the length of the ductus ejaculatorius (*2b*) and the character of the testes (*4b*), seminal vesicles (*3*), vas deferens (*4a*) and mucous glands (*2c*).

VARIATIONS AND COMBINATIONS OF THE ELEMENTS.

Various combinations of the elements of the copulatory apparatus are found in the species of allied genera. Quite a wide range of variation is also found in the character of the elements in the species of the same genus. Even species which in all other respects appear to be closely allied have very different characters, either in the form of one or more elements or in different combinations of the elements.

In Division I of the family Ipidæ the absence of the seminal valve and the presence of the seminal rod appear to predominate. The valve, as a definite part, is absent in 21 genera and 52 species and present in 10 genera and 16 species. The rod is present in 25 genera and 55 species and absent in 8 genera and 14 species. Both the rod and valve appear to be absent in 6 genera and 10 species, representing 4 subfamilies, and both are present in 10 genera and 15 species, representing the same four subfamilies, and especially in Corthylinæ. The striking feature of the Subfamily Ipinæ is the apparent[a] separation of the femora from the body, especially in *Ips* and the closely allied genera. In *Pityophthorus* (figs. 104, 105) they are found to be fused with the body in some species and separated in others; within still other species there is a supplementary band (*a3*) connecting them at or near the base.

[a] The writer has found that the femora are connected to the body by ligaments.

In Division II of the Ipidæ the presence of the seminal valve and absence of the seminal rod predominate. The valve is present in 20 genera and 44 species and the rod is absent in 20 genera and 43 spe-

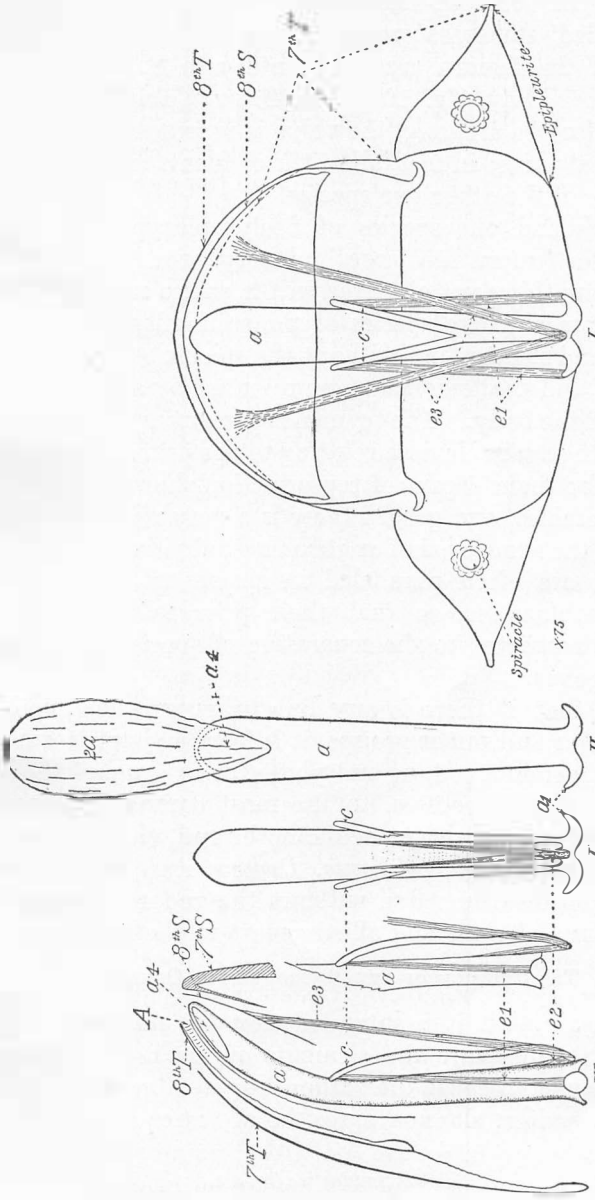


FIG. 110.—*Crossotarsus leconteï*: Posterior elements of male reproductive organs. *I*, ventral aspect; *II*, dorsal aspect; *III*, lateral aspect; *A*, anal orifice; *7th T*, seventh tergite; *7th S*, seventh sternite; *8th T*, eighth tergite; *8th S*, eighth sternite. See terminology, Division I, pp. 192–193. (Original.)

cies. The valve is absent in 2 genera and 4 species and the rod is present in 6 genera and 12 species. The combination of rod and valve is found in 4 genera and 10 species.

In the family Scolytidæ there appears to be a wide range of variation. In *Erineophilus schwarzi* Hopk., of the subfamily Hexacolinæ, the rod is absent, the valve present, and the femora are long and slender. In some species of the genus *Scolytus* the body is greatly modified, somewhat resembling a seminal rod. The valve is absent and the femora are rudimentary in *S. muticus* Say and *S. quadrispinosus* Say (fig. 109). In *S. rugulosus* Ratz., however, (fig. 108) the femora are long, the valve is represented, and there are some additional parts; in fact, all of the elements are radically different from those of the other two species.

In one genus and one species of Scolytoplatypodidæ the rod is absent and the femcra are large and very broad, differing in this respect from anything yet observed in the entire superfamily.

In two genera and five species of the subfamily Platypodinæ the body is long and slender, but without the spicule, end plates, seminal valve, or rod, and the femora are represented by short hooks at the basal angles of the body. The tegmen is present in the form of a fork.

A study of the available data relating to the primary and secondary elements of the male organs of reproduction shows that within the families, subfamilies, and genera there is a very wide range of variation and that the same or similar elements individually, or in various combinations, are often paralleled in species of widely separated genera and subfamilies, so that their principal taxonomic value appears to be restricted to the separation of species and minor divisions of the genus.

It appears that if there is any line of progressive modification within the major and minor groups, it is from a simple form without seminal valve, seminal rod, or end plates, as in some of the Cryphalinæ and in the Platypodinæ, to the most complex forms with or without the valve and with or without the rod, the rod reaching its highest development in *Xyleborus*, *Dryocœtes*, *Lymantor*, *Ips*, and allied genera; while the valve without the rod reaches its highest development in *Hylesinus* and allied genera in the Hylesininæ.

Terminology of the Reproductive Organs.

In the following list it is intended that the numbers and letters should serve to designate the elements of the reproductive organs rather than names, because the names proposed by different authors, including the writer, do not agree in all cases in designation or interpretation.

Male Reproductive Organs.

(Figs. 101–110.)

Division 1. Posterior chitinous division.
Division 2. Posterior membranous division.
Division 3. Median division.
Division 4. Anterior division.

Division 1.

a. Body.
- *a1*. Body apodemes (femora).
- *a1a*. Apodemal ligament.
- *a2*. Lateral folds.
- *a2a*. Lateral plates (accessory pieces, Nüsslin).
- *a3*. Supplementary body apodemes or transverse band.
- *a4*. Apical orifice or ejaculatory canal.
- *a5*. Sensory area or pores.

b. End plates.
- *b1*. Seminal valve and accessories.
- *b2*. Seminal rod.
- *b3*. Apical flagellum of *b2*.
- *b4*. Apical brush of *b2*.
- *b5*. Sensory claspers (fig. 108, *b5*).
- *b6*. Apical lobe.

c. Tegmen.
- *c1*. Posterior or dorsal section.
- *c2*. Anterior or ventral section.
- *c3*. Apodemal process.

d. Spicule.
- *d1*. Anterior section.
- *d2*. Posterior section.
- *d2a*. Lateral apodeme or minor prong.
- *d2b*. Lateral barb.

e. Muscles.
- *e1*. Extensors.
- *e2*. Retractors.
- *e3*. Supplementary.

f. Connecting membrane.
g. Ligament.

Division 2.

2a. Ejaculatory sac or præputial sac.
2a1. Chitinous base, or tube.
2b. Seminal duct.
2c. Mucous glands.

Division 3.

3a. Seminal vesicle.

Division 4.

4a. Vas deferens.
4b. Testes.

Female Reproductive Organs.

(Fig. 111.)

Division 1. Posterior division.
Division 2. Anterior division.

Division 1.

1a. Vagina.
1b. Bursa copulatrix.
1ba. Accessory sac.
1c. Unpaired oviduct.
1ca. Apex and apical orifice of oviduct.

1d. Spermatheca.
1e. Spermathecal gland.
1f. Seminal duct.
1g. Cement glands.
1h. Chitinous plates.

Division 2.

2a. Paired oviducts.
2b. Ovaries.

Classifications Based on the Reproductive Organs.

In the classifications of Nüsslin (1911), Fuchs (1911), and others, as based on the male reproductive organs, we find, as we do in the classifications based on the elements of any single organ, that genera and groups which are plainly not closely allied are brought together and those which by the majority of external and internal characters are closely allied have been placed in widely separated divisions or subdivisions. When, however, the facts of parallel modification are taken into consideration and the principal elements are correlated with those of other organs, the results are quite different and the true taxonomic value of the elements is recognized. It is evident that a study must be made of the male organs of reproduction in a much larger number of species of all available genera before the true taxonomic value of any of their elements can be determined and correlated.

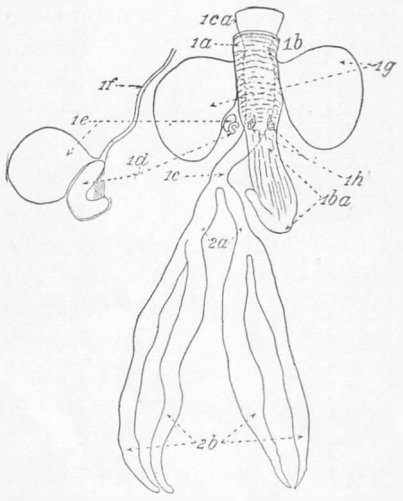


Fig. 111.—*Dendroctonus valens:* Female reproductive organs. See terminology, Division 1, pp. 193–194. (Original.)

Nüsslin (1912), who has given the subject of the female reproductive organs (Fig. 111) of Scolytidæ late consideration, calls attention to the taxonomic importance of the female genital organs in separating the Adephaga and Polyphaga of the order Coleoptera and in distinguishing the suborder Rhynchophora, which he claims is peculiar in having only two pairs of ovaria.

The absence of a true ovipositor is apparently common to all scolytoid beetles, although in some species there are rudimentary parts which in other Rhynchophora and Coleoptera belong to the ovipositor, especially the genital palpi, which have been found only in *Scolytus* and *Hylesinus*. The presence of paired or single cement glands appears to be an important and more or less peculiar element in the Scolytoidea, although it is said to be absent in *Scolytus* and *Ernoporus*, as

in other Rhynchophora. The bursa copulatrix, according to Nüsslin, is present in *Scolytus, Hylesinus, Polygraphus, Crypturgus,* and *Hypoborus,* much less evident in *Carphoborus, Pityophthorus, Dryocœtes, Taphrorychus,* and *Lymantor,* and obscure or absent in *Cryphalus, Xyloterus, Xylocleptes, Thamnurgus, Ips,* and *Pityogenes.*

Conclusions as to whether or not the presence or absence of a given element is primitive in the Scolytoidea, as based on morphological interpretations, are becoming much less reliable than formerly because of the frequency of parallel origin or disappearance of adaptive elements.

Nüsslin's (1911, pp. 333–338) classification as based on the female organs of reproduction relates primarily to the presence or absence of the cement gland and to its varying forms; secondarily, to the presence and character, or the absence, of the bursa copulatrix, and the character of the spermatheca and its seminal duct.

When the characters of the female reproductive organs as given by Nüsslin are correlated with the external characters on which the writer's preliminary classification is based, *Scolytus* falls into the subfamily Scolytinæ; *Hypoborus* and *Thamnurgus* into the Micracinæ; *Crypturgus* and *Carphoborus* into the Crypturginæ; *Polygraphus* into the Phlœotribinæ; *Pityophthorus, Pityogenes,* and *Ips* into the Ipinæ; and *Xyloterus* into the Corthylinæ; while *Ernoporus, Cryphalus, Taphrorychus, Lymantor, Dryocœtes, Xyleborus,* and *Xylocleptes* fall into the Cryphalinæ.

With a more comprehensive study of the female organs in numbers of species representing all the genera it will evidently be found that there are some excellent taxonomic characters in the primary elements and in their lines of progressive modification, which in combination with other internal and external characters will be of special value in defining groups of allied genera and in indicating relative positions of the groups in the classification.

Secondary Sexual Characters.

There is a wide range in the types and position of the secondary or external sexual characters, such as difference in the size of the body, as in *Hypothenemus, Stephanoderes, Coccotrypes, Xyleborus,* and allied genera, and the radical and contrasting differences in the structure, vestiture, and sculpture of various external parts and areas. The front of the head may be convex and glabrous in one sex and in the opposite sex it may be flat to deeply concave, smooth, and shining, punctured, and with dense and long pubescence or the margins fringed with long hairs. The armature of the declivity and the character of the sutural impressions or broad excavation often vary to a remarkable extent in the two sexes. The scape of the antenna may be stouter to dilated and fringed with long hairs or not fringed. The funicle, club, mouthparts, tibia, tarsus, abdominal tergites, and sternites, in

fact almost every important element of the body, may be the bearer of characters for distinguishing one or the other sex.

It would appear that as a rule there is a certain degree of constancy in the location and general appearance of a male or female character within the limits of a genus, but there are some remarkable differences, and even reversals, even in the major and minor divisions of a genus. In *Dendroctonus*, for example (Part I of this bulletin, p. 73), the females of subdivision *A* are distinguished by the presence of a transverse ridge on the anterior area of the pronotum, while in subdivisions *B*, *C*, and *D* this character is not present. In subdivision *B* the elytral declivity is more rugose in the female, in subdivision *C* this is reversed, and in subdivision *D* there is no difference in this respect. In some genera the pubescent or concave front is a female character, while in other genera it is a male character. Other reversals may not only occur in different, widely separated genera but in the same genus. Therefore it is not safe to conclude that because certain characters designate the female in one species this will hold true for the other species of the same genus or for allied genera. This can only be definitely settled by dissection, which can be done without seriously mutilating the specimen if the abdomen is carefully removed from the body and the sternites are remounted on a card point after the examination is made. The presence of the chitinized spermatheca in the female and the presence of the chitinized elements of the posterior section of the male organs are sufficient to settle the point, even in old dried specimens.

The lines of progressive variation or modification in secondary sexual characters appear to range from absent and obscure to common and prominent.

THE PUPÆ.

Comparatively very little study has been made of the pupæ of even our common species of Scolytoidea, and until a comprehensive study has been made it is scarcely necessary to mention the characters in connection with general taxonomy. The description and figures of the pupa of *Dendroctonus valens* (Part I, pp. 53–57, figures 37–38; synopsis, pp. 73–74, and descriptions, pp. 81–152) will serve as an example of the general type, while the figures and terminology will serve as a guide to future study.

The writer has examined the pupæ of quite a large number of North American species and finds that there is quite a wide range of variation, but no attempt has been made to analyze the taxonomic characters except in the genus *Dendroctonus*, in which the form of the head and the character of the frontal, tergal, lateral, pleural, caudal, and femoral spines serve as important characters for identification and classification and, when correlated with the adult characters, give the same or similar taxonomic result.

THE LARVÆ.

The structural and morphological elements of the larvæ of *Dendroctonus* are shown in Part I, figures 39–43, and Plate VIII, figures 1–23*j*, and these, with the terminology and descriptions, will serve as a guide to a greatly needed further study of the larval stage before we can have a basis for conclusions as to their importance in taxonomy. The writer has examined the larvæ of quite a large number of species, but no detailed study has been made except in *Dendroctonus* and of the labrum of a number of species in other genera (Hopkins, 1905, Plate I). This has been sufficient, however, to indicate the wide range of variation in some of the elements and the great importance of a more comprehensive knowledge of the subject. In *Dendroctonus* the important characters are found in the eighth and ninth abdominal tergites, and the front of the head. An example of progressive modification is found in the sculpture and armature of the eighth and ninth abdominal tergites from those without dorsal plates in Division I and Division II, section a^3, to the unarmed plates of section a^4 and to the armed plates of subdivision *D*, which correlates so nicely with progressively modified characters in the adults and in the galleries. The larvæ of the species of *Platypus* and *Crossotarsus* examined by the writer show radical differences in form and in some of the anatomical elements, as, for example, the labrum (Hopkins, 1905).

THE EGGS.

While the eggs of many species have been observed by the writer, they have not been studied in detail. They appear to conform in general to an oblong, oval, or nearly globular shape, and are pearly white and smooth, with few elements of vestiture or sculpture to serve as taxonomic characters. However, this is a subject worthy of detailed study. The size of the egg in comparison with the size of the abdomen varies enormously in different species. In a species of *Carphoborus* a fully developed single egg was found to be so large as to occupy almost the entire abdominal cavity.

THE EMBRYO.

The embryology of the scolytoid beetles is another subject which has not received much attention. While the writer feels that there is need of detailed study of the embryo to determine any additional facts which may be of value, he is inclined to the belief that more attention should be given to a comparative study and correlation of characters of the postembryonic stages (young to matured larvæ) of a wide range of species in the order Coleoptera, in order that we may know something more of the fundamental facts and be better able to interpret their real significance.

PHYSIOLOGICAL CHARACTERISTICS.

As pointed out in Part I (p. 64), the physiological characteristics are of special taxonomic importance when correlated with morphological characters. The food, social, and sexual habits, character of the brood galleries, choice of host plants, and distribution of genera and species are all more or less rich in facts of taxonomic importance.

GENERAL HABITS.

The scolytoid beetles are distinguished from nearly all other Rhynchophora by their habit of excavating characteristic egg galleries in the living or dead plant tissue. The few notable exceptions are found in the genus *Stenoscelis*, of the Calandridæ, the adults of which excavate a primary egg burrow, but as a rule this habit within the suborder is peculiar to the Scolytoidea. The egg galleries of Scolytoidea are excavated in the bark or wood of trees and shrubs, the roots, stems, and leaves of herbaceous plants, the fruits or seeds of palms and other plants, young pine cones, the wood of barrels or casks containing water or spirituous liquors, etc. Some of the species excavate their galleries in decaying bark or wood or even in the fruiting bodies of fungi, while others confine their work to the bark or wood of weakened, dying, or recently dead plants, and still others prefer to enter the living and sound tissues.

The food of the adults and larvæ consists of the sugars, starches, and other nutritive elements of their host plants, or of fungi which grow in their brood galleries.

CLASSIFICATION ACCORDING TO HABITS.

Any classification of the families or subfamilies based on food habits alone would not indicate a natural arrangement, as is plainly indicated by the parallel habits of groups of species in widely separated families, subfamilies, and genera. It is true that there are several well marked classes according to habits, such as bark beetles, twig beetles, seed beetles, cone beetles, and ambrosia beetles. It is evident, however, that food habits, like many other characteristics and structural characters, have evolved along parallel lines in allied as well as in widely separated groups. There are many examples illustrating this principle. The genera *Xyleborus*, *Corthylus*, *Scolytoplatypus*, and *Platypus* are, according to fundamental morphological elements as well as groups of correlated characters, so widely separated that they each represent a different family or subfamily; yet the habit of excavating their galleries in wood and feeding on ambrosial fungi is common to them all. Between some of these genera there is also a more or less constant resemblance in certain morphological characters, especially in the hairs and slender teeth of the

lacinia of the maxilla, but this is evidently due to parallel adaptation to similar uses and not to common origin or phylogenetic descent from a common ambrosia-feeding ancestor.

Food Habits of the Adults.

As a rule the adults obtain their food from the substance in which they excavate their egg galleries or from the fungi growing on the walls of the galleries, but there are numerous examples of special food habit such as that found in *Scolytus*, *Pteleobius*, *Phlœosinus*, and *Tomicus* (see p. 220), which excavate food burrows in the living twigs of their host trees.

Food Habits of the Larvæ.

There is a wide range of variation in the food habits of larvæ of different species, especially in the character of their food burrows or larval mines. Each species of a group of closely allied species may have similar habits, but, as shown in the genus *Dendroctonus*, there may also be a wide range of variation and some striking examples of progressive modification in this habit within a genus in which there is a restricted range in structural characters in the adults. In the genus *Dendroctonus* there is a tendency throughout for the larval mines to occur in groups of increasing numbers from the simple, isolated mine of *Dendroctonus brevicomis* to closely placed groups in *Dendroctonus simplex* and *D. piceaperda* and to the large social chamber of *micans*, *valens*, and *terebrans*. (See figs. 73, 75, 79, 88, and 91, of Part I.) Thus the stage in the modification of the larval mine of a given species may indicate, in connection with stages in the modification of structural characters, the natural position of the species.

In the ambrosia beetles the larvæ of some species and groups of genera, as *Xyleborus*, *Stephanoderes*, and *Crossotarsus*, live in the primary galleries in direct association with the eggs, larvæ, pupæ, young adults, and parent adults, while in the subfamily Corthylinæ, the genus *Scolytoplatypus*, and at least some of the species of *Platypus*, the larvæ occupy separate chambers in the sides of the gallery, these chambers not extending beyond a size sufficient for the accommodation of the body.

Pupal Habits.

Considerable variation exists in the habits of the pupæ and in the cells occupied by them in transformation from larvæ to adults. In perhaps the majority of species the transformation takes place at the end of the food burrow with or without a definite cell. In some ambrosia beetles the pupation takes place in the social galleries occuped by different stages of the brood, in others it is in the lateral larval cell, and in *Stephanoderes* the transformation takes place in closely joined

cells at or toward the inner end of the social gallery, the walls and partitions of these cells consisting of an ambrosia-like substance mixed with fine borings.

Flight Habits.

Further observations should be made on the flight habits of these beetles, but from what we know of a few species it would appear that in the same species flight may be either individual or collective. In one example noted by the writer (Hopkins, 1899a, pp. 346–348), a large number of species, together with some of their associates, scavengers, and predaceous enemies, were found in one great swarm. The periods of flight vary with the number of generations in a season. Thus species with a single generation have but one definite period of flight, while those with more than one generation have two or more periods, or, when the generations overlap, there may be a continuous period of flight throughout the season.

Social Habits.

In the social habits we find some features of special interest both in their relation to taxonomy and to parallel lines of modification. In the relation of the sexes there is a wide range of variation from simple or unorganized and intensive polygamy to specialized or organized polygamy, and a gradual reduction in the proportion of the number of females, from 1 male and many females to 1 male and 2 females, and finally to specialized monogamy.

In *Hypothenemus, Stephanoderes, Xyleborus,* and allied genera the males are much smaller than the females and very rare. In certain species of *Xyleborus* as many as 60 females to 1 male have been found in one brood gallery, and the proportion appears to be even greater in *Hypothenemus.* In these groups there is no system in the relation of the sexes or in eggs of the brood galleries of the females, and all live together in the same galleries. In the other groups of genera of the subfamily Cryphalinæ where there is no difference in the size of the sexes there is more evidence of separate egg galleries for the different females of the social group, and the galleries begin to take on more definite and characteristic forms or patterns. In the Ipidæ the tendency toward a specialized polygamous relation of the sexes reaches its highest development in *Pityogenes,* while in *Ips* there is a tendency toward fewer females, the numbers of which in some cases are limited to 2 or 3 to the gallery. In Corthylinæ the sexes are more equally divided, while in Crypturginæ, Phlœotribinæ, and Hylesininæ there is a tendency toward 2 females and 1 male or to 1 of each. The last seems to prevail to a greater extent in the subfamily Scolytinæ, or at least in the genus *Scolytus,* than in other subfamilies.

Galleries.

There is a wide variation in the types or forms of the egg and brood galleries within the families, subfamilies, and the major and minor groups, and in some cases within the genus. Each species or group of allied species of a genus or group of allied genera is usually characterized by some peculiar form or feature which in many cases is sufficent in itself to indicate the species, genus, or group to which it belongs; therefore the galleries are of special taxonomic importance in indicating the natural position and grouping of the species and genera.

It has been supposed that a peculiar type of gallery was due to the character of the plant tissue in which it was excavated or that it had some relation to the species of plant. It is found, however, that the type of the gallery is the same, or similar, for the same species, regardless of the character of the substance or the species of plant in which it is excavated. In fact, the same species of spruce or pine, and the bark on the trunk or branches, or the wood of the same part of the tree, may have as many radically different types of galleries as there are different species of beetles to make them.

It has also been supposed that the type of a gallery was due to the peculiar structure of the beetles, such as the retuse or concave and armed elytral declivity in *Ips*, ascending or excavated abdominal sternites of *Scolytus*, etc., but it is found that certain species with the same or similar structures make very different types of galleries, while certain other species with very different structures make similar galleries.

The fact that there is quite a definite relation between the type of the gallery and the systematic position of the species, genus, and group would indicate that the evolution of the gallery has been from the simple to the complex and that it has progressed with the evolution of the beetles that make and inhabit it in a somewhat similar manner to that of the dominant tendency in the evolution of human dwelling places from the simple cave to the modern palace. In other words, the simple and complex galleries represent evolution within the maximum and minimum limits of an instinctive or dominant tendency common to all of the individuals of the superfamily Scolytoidea and are expressed by each species of a genus in the varying degrees of simplicity or perfection according to the varying stages in the evolution of the species.

The fact that the same or a similar type of gallery is made by species of widely separated genera and subfamilies indicates that we should not look for an explanation of the origin and evolution of types of galleries in the phylogeny of the species, but that a thorough consideration should be given to the explanation to be found in paral-

lel evolution due to a common tendency which may lead to the same or similar results during the same or similar stage in the evolution of the species.

While the varying types of the egg and brood galleries furnish some very important taxonomic evidence, any attempt to classify the species of a family or subfamily according to such characters alone would give the same heterogeneous results as are found in the different classifications based on the elements of a single external or internal part or organ of the body. On the other hand, if the galleries of the species of the major and minor divisions of a subfamily are studied separately, it will be found that the character of the gallery and the species of the host tree will serve as most important guides to the natural position of a species or group of allied species.

TERMINOLOGY OF THE GALLERIES.

Following is a revised list with definitions of the terms used to designate the different elements of the scolytoid gallery.

Egg gallery.—The egg gallery is the burrow excavated by the parent beetles preliminary to depositing the eggs in niches along the sides or loosely in the gallery itself.

Social gallery.—The social gallery is one in which all stages of the broods from the eggs to the matured individuals and the parents live, as in *Xyleborus*, certain species of *Platypus*, *Crossotarsus*, etc.

Social chamber or brood chamber.—The social chamber, as in *Xyleborus saxeseni*, is a dilated portion of the tubelike gallery to accomodate all stages of the brood.

Death chamber (*catacomb or garbage chamber*).—The death chamber (Hubbard, 1897; also Hopkins, 1898) is a section in the social chamber in which the dead individuals of the colony or the guests and enemies as well as other refuse matter are deposited and separated from the main chamber by a wall of the ambrosia fungus mixed with boring dust.

Entrance burrow.—The entrance burrow is made by one or the other sex as a preliminary to the excavation of the egg gallery, and may connect in a direct manner or laterally with the base of the gallery in the case of single galleries, or with the middle in the case of double galleries.

Nuptial (*lateral or central*) *chamber.*—The nuptial chamber is excavated by one or the other sex (probably in most cases by the male) at the base of the entrance burrow and the mouth of a single or many egg galleries. In *Pityophthorus*, *Ips*, etc., this chamber is short and broad, oblong, or rectangular. In some species of *Scolytus*, *Phlœophthorus*, *Hylesinus*, etc., the lateral entrance appears to serve the same purpose as the nuptial chamber, while in *Phlœosinus* the chamber is at the base of the egg galleries and entrance burrow and

extends to one or both sides. These chambers are usually occupied by the male of the polygamous colony or of the monogamous pair.

Ventilating burrow.—The ventilating burrow is the vertical burrow which is located at more or less regular intervals in the roof of the egg gallery and extends to or near the surface. It may serve the purpose of ventilating the gallery, or, perhaps more frequently, as a place for the storage of boring dust or an opening through which this dust may be ejected. Short burrows in the roof or sides may be used as places in which the beetles turn around, or may serve the purpose of nuptial chambers.

Branching gallery.—The branching gallery may branch from the central or nuptial chamber, or from the side of one of the main egg galleries. In the latter case it is referred to as a lateral branch.

Connecting galleries.—The connecting galleries are those of one or more colonies which are connected either through the central chamber or by lateral and primary galleries, as in many species of *Pityogenes, Pityophthorus, Carphoborus,* etc.

Terminal burrows.—The terminal burrows are excavated usually by the female beetle at the farther end of a primary or a lateral gallery, after the egg gallery is completed and while the brood is developing, as in *Dendroctonus frontalis* (Part I, figs. 51 and 52).

Brood burrows.—The brood burrows are those excavated by the adults of a brood before the individuals emerge. They radiate from the respective pupal cells of the individuals, as in *Dendroctonus,* certain species of *Ips,* etc. In the case of species with a single generation annually, the developed brood may overwinter in the brood burrows.

Hibernating burrows.—The hibernating or overwintering burrows are those excavated in places other than that in which the broods developed, such as those of *Ips,* in the twigs and branches, or in the thick corky bark at the base of the trees, and those of *Phlœophthorus,* in the outer bark on the trunks of the living host trees.

Food burrows.—The food burrow is excavated by the adult in the same part of the tree in which it excavates its egg galleries, or in a different part, as in *Scolytus rugulosus* and *S. quadrispinosus,* which burrow in the living twigs at the base of a leaf stem or bud, and in *Phlœosinus,* which burrows at the base of living twigs.

Trial burrows.—The trial burrows are those made by the parent beetles in the bark of living trees preliminary to the general attack and the excavation of successful egg galleries.

Abandoned or failure gallery.—The abandoned or failure gallery is one which, through the resistance exerted by the vital part of the plant attacked, the beetles are compelled to abandon or be drowned in the resin or sap.

chambers at base; (*c*) regular, short or long, with lateral entrance chambers at base; (*d*) the most highly specialized short or long type, without lateral entrance chambers at base.

The foregoing classification and terminology is based on the observed galleries of a large number of species representing 57 genera and includes the galleries of European species figured by other writers.

RELATION OF TYPES OF GALLERIES TO THE SUBFAMILIES AND FAMILIES.

The relation of the eight groups of galleries to the subfamilies is shown in the following table. In some cases one genus may be represented by several groups. In *Pityophthorus* 26 species are represented in groups 1, 4, and 5, and in *Ips* 39 species are represented in groups 2, 4, and 5.

TABLE VI.—*Relation of groups of galleries to the subfamilies in the Scolytoidea.*

Subfamilies.	Groups of gallery types and number of genera in each group.							
	1	2	3	4	5	6	7	8
Ipidæ:								
Division I—	*Genera.*	*Genera.*	*Genera.*	*Genera.*	*Genera.*	*Genera.*	*Genera.*	*Genera.*
Cryphalinæ	4	4	3					
Ipinæ	1	1		3	3	2		
Corthylinæ			5					
Micracinæ					1		2	
Division II—								
Cryptarginæ	2							1
Phlœotribinæ				2	1	2		2
Hylesininæ	2	2				8	2	7
Scolytidæ:								
Hexacolinæ					1			
Bothrosterninæ							1	
Scolytinæ						1	1	1
Scolytoplatypodidæ:								
Scolytoplatypodinæ			1					
Platypodidæ:								
Platypodinæ			2					

This table shows that all of the simple types (1 and 2) are in the Ipidæ and that most of them fall in the first part of Division I, while the more specialized types fall in the last part of Divisions I and II, with the far greater number in the latter; also, that in Scolytidæ specialized types only have been found. It is probable, however, that simple types will be found in the Scolytidæ when we know more about the habits of the species of the other genera of this family. It is also interesting to note from Table VI the number of subfamilies and genera in which the same group types are paralleled.

extends to one or both sides. These chambers are usually occupied by the male of the polygamous colony or of the monogamous pair.

Ventilating burrow.—The ventilating burrow is the vertical burrow which is located at more or less regular intervals in the roof of the egg gallery and extends to or near the surface. It may serve the purpose of ventilating the gallery, or, perhaps more frequently, as a place for the storage of boring dust or an opening through which this dust may be ejected. Short burrows in the roof or sides may be used as places in which the beetles turn around, or may serve the purpose of nuptial chambers.

Branching gallery.—The branching gallery may branch from the central or nuptial chamber, or from the side of one of the main egg galleries. In the latter case it is referred to as a lateral branch.

Connecting galleries.—The connecting galleries are those of one or more colonies which are connected either through the central chamber or by lateral and primary galleries, as in many species of *Pityogenes, Pityophthorus, Carphoborus,* etc.

Terminal burrows.—The terminal burrows are excavated usually by the female beetle at the farther end of a primary or a lateral gallery, after the egg gallery is completed and while the brood is developing, as in *Dendroctonus frontalis* (Part I, figs. 51 and 52).

Brood burrows.—The brood burrows are those excavated by the adults of a brood before the individuals emerge. They radiate from the respective pupal cells of the individuals, as in *Dendroctonus,* certain species of *Ips,* etc. In the case of species with a single generation annually, the developed brood may overwinter in the brood burrows.

Hibernating burrows.—The hibernating or overwintering burrows are those excavated in places other than that in which the broods developed, such as those of *Ips,* in the twigs and branches, or in the thick corky bark at the base of the trees, and those of *Phlœophthorus,* in the outer bark on the trunks of the living host trees.

Food burrows.—The food burrow is excavated by the adult in the same part of the tree in which it excavates its egg galleries, or in a different part, as in *Scolytus rugulosus* and *S. quadrispinosus,* which burrow in the living twigs at the base of a leaf stem or bud, and in *Phlœosinus,* which burrows at the base of living twigs.

Trial burrows.—The trial burrows are those made by the parent beetles in the bark of living trees preliminary to the general attack and the excavation of successful egg galleries.

Abandoned or failure gallery.—The abandoned or failure gallery is one which, through the resistance exerted by the vital part of the plant attacked, the beetles are compelled to abandon or be drowned in the resin or sap.

Exit burrow.—The exit burrow is that through which one or many individuals of a developed brood emerge. In the case of ambrosia beetles the entrance may also be utilized as an exit, but in the bark-beetles the exit is usually direct or indirect from the pupal chamber.

Larval mine.—The larval mine is the food burrow excavated by the larvæ from the point where it hatches from the egg. The individual mine may be widely separated from or closely approximate to those of other individuals of the same brood, and they may be arranged in groups or those of the entire brood may be connected to form one common larval chamber.

Larval cell.—The larval cell is excavated by the larvæ in the side of the gallery simply to accomodate the increasing size of the body, as in the case of many species of Corthylinæ where the food consists of ambrosial fungi provided by the parent.

Pupal cell.—The pupal cell is formed by the prepupal larva or by the pupa itself and is usually located at the end of the larval mine or food burrow of the larva. This is especially true in the case of the barkbeetles or the wood-mining larvæ, which latter, as in *Micracis*, *Thysanoes*, *Scolytus muticus*, etc., extend their burrows for a long distance from the bark mines into the wood. On the other hand, certain species of *Dendroctonus* form the pupal cell in the outer corky bark (*D. frontalis*) or in the social larval chamber (*D. valens*), instead of at the end of the larval mine as in *D. ponderosæ*.

All of the named parts of the gallery have characters more or less peculiar to the species or group of allied species. Therefore the galleries as a whole, or in their various elements individually, or in various combinations, are worthy of special attention in the search for taxonomic characteristics.

CLASSIFICATION OF THE GALLERIES.

Egg Galleries.

In an attempt to classify the scolytoid egg galleries it is important to remember that the newly excavated galleries in which the first sets of eggs are deposited are more reliable in suggesting the type or group they represent than are the older ones, because in some species they may be so radically changed and confused by secondary branches and the intermingling of two or more galleries that the characteristic type may be obscured.

Larval Mines.

The larval mines furnish, to a limited extent, evidence of progressive modification, as is found in *Dendroctonus*. The larval mines in most of the Cryphalinæ are without distinctive characters, while in Ipinæ, Hylesininæ, and Scolytinæ their symmetrical arrangement

represents a high stage of progress, and consequently they are more characteristic of the species.

The form of the egg gallery of any species consists of one or more of three primary elements in relation to the substance and its fiber in which the gallery is made, as follows: (1) The longitudinal gallery, (2) the transverse gallery, and (3) the broad, irregular chamber.

Types and Subtypes of Egg Galleries.

The various modifications and combinations of the three primary elements seem to represent 8 general types or groups, which are designated by numbers, and 32 more specific subtypes or forms, which are designated by letters, as follows (see fig. 112):

Group 1.—The simple or generalized type. (*a*) Simple, longitudinal; (*b*) simple, transverse; (*c*) simple cavities; (*d*) various combinations of *a* and *b*, with lateral branches.

Group 2.—The simple, irregular type branching from an irregular central or basal chamber. (*a*) Long, longitudinal, branching; (*b*) short, sublongitudinal, branching; (*c*) short, transverse, branching; (*d*) various combinations of *b* and *c*.

Group 3.—Ambrosia galleries. *Division I, without lateral larval chambers.* (*a*) Simple, longitudinal, single or branching; (*b*) long, transverse, branching; (*c*) short,

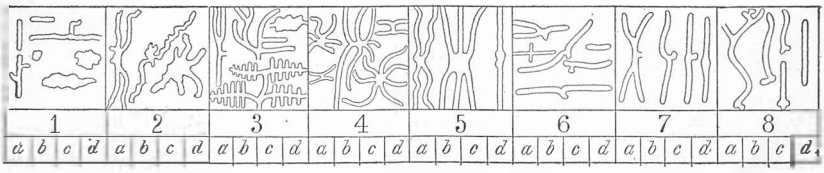


FIG. 112.—Classification of galleries of Scolytoidea. (Original.)

transverse, branched, dilated. *Division II, with lateral larval chambers.* (*d*) Double, transverse, branching;

Group 4.—The specialized, intermediate, short type, branching from a regular central nuptial chamber. (*a*) Simple to complex, transverse; (*b*) simple to complex, sublongitudinal; (*c*) intermediate combinations of *a* and *b*; (*d*) complex, symmetrical combinations of *a* and *b*.

Group 5.—The specialized, intermediate, long, longitudinal type, branching from a regular central chamber. (*a*) Simple, irregular types with few branches; (*b*) specialized, many-branched types; (*c*) specialized, with few branches, usually three; (*d*) specialized, double, longitudinal.

Group 6.—The specialized, short, transverse type. (*a*) Simple, irregular, single or double, transverse or subtransverse, and sometimes branching; (*b*) intermediate, regular, double, transverse or subtransverse; (*c*) specialized, regular, double or single, transverse, with or without lateral entrance chamber.

Group 7.—The specialized, short, double, longitudinal type. (*a*) Irregular, branched (*Micracis*) type; (*b*) irregular, without branches, but with lateral entrance chambers; (*c*) intermediate, more specialized, with or without lateral entrance chambers; (*d*) highly specialized, without lateral entrance chambers.

Group 8.—The specialized long or short, single, longitudinal type. (*a*) Long, irregular, winding, sometimes with lateral branches, with or without lateral entrance chambers at base; (*b*) short, irregular, without branches, but with lateral entrance

chambers at base; (*c*) regular, short or long, with lateral entrance chambers at base; (*d*) the most highly specialized short or long type, without lateral entrance chambers at base.

The foregoing classification and terminology is based on the observed galleries of a large number of species representing 57 genera and includes the galleries of European species figured by other writers.

RELATION OF TYPES OF GALLERIES TO THE SUBFAMILIES AND FAMILIES.

The relation of the eight groups of galleries to the subfamilies is shown in the following table. In some cases one genus may be represented by several groups. In *Pityophthorus* 26 species are represented in groups 1, 4, and 5, and in *Ips* 39 species are represented in groups 2, 4, and 5.

TABLE VI.—*Relation of groups of galleries to the subfamilies in the Scolytoidea.*

Subfamilies.	Groups of gallery types and number of genera in each group.							
	1	2	3	4	5	6	7	8
Ipidæ:								
Division I—	*Genera.*	*Genera.*	*Genera.*	*Genera.*	*Genera.*	*Genera.*	*Genera.*	*Genera.*
Cryphalinæ	4	4	3					
Ipinæ	1	1		3	3	2		
Corthylinæ			5					
Micracinæ					1		2	
Division II—								
Crypturginæ	2							1
Phlœotribinæ				2	1	2		2
Hylesininæ	2	2				8	2	7
Scolytidæ:								
Hexacolinæ					1			
Bothrosterninæ							1	
Scolytinæ						1	1	1
Scolytoplatypodidæ:								
Scolytoplatypodinæ			1					
Platypodidæ:								
Platypodinæ			1					

This table shows that all of the simple types (1 and 2) are in the Ipidæ and that most of them fall in the first part of Division I, while the more specialized types fall in the last part of Divisions I and II, with the far greater number in the latter; also, that in Scolytidæ specialized types only have been found. It is probable, however, that simple types will be found in the Scolytidæ when we know more about the habits of the species of the other genera of this family. It is also interesting to note from Table VI the number of subfamilies and genera in which the same group types are paralleled.

TABLE VII.—*Relation of groups of galleries to the families of Scolytoidea.*

Groups.	Ipidæ.		Scolytidæ.	Scolytoplatypodidæ.	Platypodidæ.
	Division I.	Division II.			
	Genera.	*Genera.*	*Genera.*	*Genera.*	*Genera.*
1.....	5	5	0	0	0
2.....	4	3	0	0	0
3.....	9	0	0	1	2
4.....	3	2	0	0	0
5.....	4	1	1	0	0
6.....	2	8	1	0	0
7.....	3	2	2	0	0
8.....	0	9	1	0	0

In *Hypothenemus* the types of galleries do not extend beyond group 1 and represent specific types *a*, *b*, *c*, and *d*; *Cryphalus* is also confined to the same group and types, while *Pityophthorus* represents group 1, *a* and *d*; group 4, *a*, *b*, *c*, and *d*; and group 5, *a* and *d*. *Ips* represents group 2, *a*, *b*, *c*, and *d*, and group 5, *a*, *b*, *c*, and *d*.

The relation of types of galleries to species shows some striking examples of progressive modification within a genus and of parallel characters in different genera. It is not desirable to present a table to illustrate these relations in this connection, but it is intended to do so in subsequent parts dealing with the subfamilies.

While considerable attention has been given to the subject, a far more comprehensive study of the egg and brood galleries than has yet been made is required as a basis for correlating their taxonomic characters with the morphological characters of the species.

TAXONOMIC RELATION BETWEEN THE BEETLES AND THEIR HOST PLANTS.

Among the scolytoid beetles there is often a close taxonomic relation between the species, genera, and groups of the beetles and the species, genera, or groups of plants they infest, so that we may often know the insect by the host, or the host by the insect.

In other words, the host, together with the character of the gallery of a beetle, will often not only serve to identify the species to which it belongs but will indicate its systematic position. In a like manner the presence of certain species of beetles will serve to identify the species of plant and indicate its systematic position.

PART OF PLANT SELECTED BY THE BEETLES.

The part of the plant in which the egg galleries are excavated is also of interest. In some species it is limited to the root or stem of an herbaceous plant; in others to the bark on the roots, main trunk, larger branches, and smaller branches, or to the twigs or fruit of a

shrub or tree. Indeed it is found that the species of an entire genus of beetles may confine their breeding places to a restricted part of the plants of a single genus or closely allied group. Therefore even the part of the plant infested by a species may be of considerable taxonomic importance in indicating the natural position of a species or genus of heretofore doubtful position.

Condition of the Plant.

The condition of the plant or plant tissue at the time it is occupied by the beetles is of considerable systematic and economic importance. It ranges from young to old plants, living, declining, dying, and dead, and to different stages of decay of the plant or some part of its tissue. The fact that there is a relation between the species of beetles and one or more of the conditions mentioned shows that there is something of taxonomic value in this phase of the subject.

Relation of the Species of Beetles to the Systematic Position of Their Host.

The primary and minor divisions and groups of plant species represented in which one or more species of beetles live range from the fruiting bodies of certain fungi of the Eumycetes to the higher flowering shrubs and trees of the Angiospermæ, the greater number of species and genera being confined to the Pinaceæ of the Gymnospermæ and the shrubs and trees of the Dicotyledoneæ of the Angiospermæ.

Range of Host Plants.

The range of host plants in the families of the Scolytoidea may be designated as follows:

Table VIII.—*Range of host plants in the families of Scolytoidea.*

Family in the Scolytoidea.	Group of host plants.			
	Fungi.	Gymnospermæ.	Monocotyledoneæ.	Dicotyledoneæ.
Ipidæ	Rare	Common	Rare	Common.
Scolytidæ	None	Rare	None	Do.
Scolytoplatypodidæ	do	None	do	Rare.
Platypodidæ	do	Common	do	Common.

The range of host plants in the genera of true barkbeetles is usually more restricted and characteristic than in the genera of ambrosia beetles or in those species which live in dead or decaying bark or wood.

Examples of restricted range of host plants.—In the Cryphalinæ we find that *Cryphalus* is partial to *Abies* and *Picea; Trypophlœus* to

Alnus, Salix, and *Populus.* In Ipinæ the true *Pityogenes* and *Ips* are largely confined to *Pinus* and *Picea.* In Corthylinæ the genus *Gnathotrichus* is confined to the *Pinus* group, while *Monarthrum* is partial to the dicotyledonous trees. In Crypturginæ the species of *Crypturgus, Dolurgus,* and *Dendroctonus* are confined to *Pinus* and allied genera. In Hylesininæ *Tomicus* (*Myelophilus*), *Hylurgus,* and *Hylastes* are confined to *Pinus,* while the true *Hylesinus* and *Pteleobius* are particularly associated with *Fraxinus.*

Examples of wide range of host plants.—In Cryphalinæ *Hypothenemus* has a range of host plants from fungi up through many genera of the Monocotyledoneæ and Dicotyledoneæ but is rarely found as an inhabitant of the Gymnospermæ. *Xyleborus* has the widest range of all—through the Coniferæ and Angiospermæ. *Dryocœtes* is divided between the conifers and allies of *Quercus.* In Corthylinæ the genus *Xyloterus* is divided between the Gymnospermæ and a wide range of the trees of the Angiospermæ. *Corthylus* is confined to a wide range of trees in the Angiospermæ, as is also *Monarthrum,* except in the case of a few records from the *Pinus* and *Juniperus* groups. In Scolytinæ the genus *Scolytus* as at present recognized is divided between the genera of the Pinales (except *Pinus*) and the Amentales and Rosales. In Platypodinæ there is a wide range of food plants in the trees of the Gymnospermæ and Angiospermæ.

Associations of Species of Beetles and Species of Plants.

In some of the genera which are restricted in the range of host plants as well as in those with the widest range there are many species which are restricted to a single species or group of closely allied species of plants. In Phlœotribinæ there are species peculiar to *Morus, Celtis,* etc., and in *Phlœosinus,* with but very few exceptions, each species is peculiar to, or prefers, a different species of cypress, cedar, or juniper, or group of allied species. In *Scolytus* we find *Hicoria, Ulmus, Fagus, Betula, Celtis, Quercus, Abies, Picea, Pseudotsuga taxifolia,* etc., with species of beetles peculiar to each plant genus.

Summary of Taxonomic Evidence Furnished by Host Relations.

In a study of the relations between the insects and their hosts some rather striking facts have been determined which have furnished evidence to clear much of the confusion in classification based on morphological characters alone and in which parallel or analogous characters have been mistaken for those of affinity. By the old method of morphological distinction closely allied species and genera have been widely separated in the classification and distantly related ones placed together. A number of such cases have been detected where the host plant and the character of the galleries have been studied.

In other words, the physiological characteristics gave the best clue to the natural affinities of the various groups and led to the discovery of heretofore overlooked morphological characters which furnished conclusive evidence of their true position.

The close relationship between some of the existing representatives of ancient groups of plants and representatives of evidently ancient types of the beetles indicates that the beetles and plants may have been closely associated in their evolution from their respective primitive forms.

GEOGRAPHICAL DISTRIBUTION IN ITS BEARING ON TAXONOMY.

Superfamily SCOLYTOIDEA.

It is evident from our present knowledge that the superfamily Scolytoidea is represented to a greater or less extent in every section of the world where woody plants grow.

Family IPIDÆ.

The family Ipidæ is also represented by species in all of the great faunal regions. The subfamily Cryphalinæ, with its widely distributed *Hypothenemus*, *Stephanoderes*, and *Xyleborus*, has a wider range of distribution perhaps than is found in any of the other subfamilies. The Ipinæ are more restricted to the Holarctic regions and to the distribution of *Pinus* and its allies, *Abies*, *Picea*, *Larix*, etc. The Corthylinæ are more restricted to temperate, subtropical, and tropical America except in the genus *Xyloterus*, which extends through the Palæarctic and Nearctic regions. The Micracinæ, with the exception of *Liparthrum* and *Hypoborus*, are largely restricted to north temperate America. In Crypturginæ the genus *Aphanarthrum* is restricted to Madeira and the Canary and Cape Verde Islands, while *Crypturgus* has a wide range through the Palæarctic and Nearctic regions, and *Dendroctonus*, with one exception, is confined to North and Central America. The Phlœotribinæ and Hylesininæ are widely distributed throughout the regions of tree growth.

Family SCOLYTIDÆ.

The family Scolytidæ, as represented by the genus *Scolytus*, extends over a wide range of the Palæarctic and Nearctic regions, but the greater number of genera and species are evidently to be found in the subtropical and tropical regions of Central and South America.

Family SCOLYTOPLATYPODIDÆ.

The family Scolytoplatypodidæ, so far as known, is restricted to small sections of the eastern Palæarctic and of the Ethiopian regions.

Family PLATYPODIDÆ.

The family Platypodidæ has a wide range through the temperate, subtropical, and tropical regions of both continents.

There are many features in the distribution of genera and species which are of special interest, but there is need of information on many species from the different countries which at present are poorly or not at all represented in collections.

PAIRED SPECIES.

The subject of so-called paired or parallel species is of special interest in connection with a study of the distribution. There are some striking examples of paired species in the genus *Dendroctonus* which, if they occupied the same local faunal area, would be difficult of separation on account of their close resemblance in structural characters. These paired species are *brevicomis* and *barberi, frontalis* and *arizonicus, mexicanus* and *parallelocollis, monticolæ* and *ponderosæ, piceaperda* and *engelmanni, punctatus* and *micans,* and *terebrans* and *valens.* In each case the pairs are more or less widely separated from each other in their geographical distribution, as, for example, *micans* of northern Europe and *punctatus* of the Appalachians of North America, *frontalis* of the Southern States and *arizonicus* of Arizona, *barberi* of Arizona and New Mexico and *brevicomis* of the Pacific Slope States, Idaho, Montana, and part of Wyoming, *ponderosæ* of the central and southern Rocky Mountains and *monticolæ* in the Northern Rocky Mountains and Pacific Slope.

There are any number of similar cases of so-called paired species in other genera, and the supposition that some of them are one and the same species has led to considerable confusion concerning the true range of a species. Between North America and Europe we have several examples, such as *Anisandrus pyri* of America and *Anisandrus dispar* of Europe, *Dryocœtes autographus* of Europe and *Dryocœtes septentrionis* of the western coast and Alaska of America, *Xyloterus lineatus* of Europe and *Xyloterus bivittatus* of America, *Hylurgops glabratus* of Europe and *Hylurgops pinifex* of America. There are many others common to two or more countries which superficially seem to be the same.

REVIEW OF TAXONOMIC CHARACTERS AND CHARACTERISTICS.

In a review of the foregoing discussion of the morphological characters to be found in the different stages of the scolytoid beetles and of the physiological characteristics in their habits, it is shown that there is a wide range of taxonomic elements by which to distinguish species and genera and to indicate or fix their position in the classification. Indeed the vast number of these characters and characteristics

and the wide range in their variation, together with the disturbing factors, or reversals, and parallel modifications, are enough to overwhelm, confuse, and discourage anyone who attempts to study and utilize them in a comprehensive classification. It is plain, however, that it is only through such a comprehensive treatment that we can hope to approach the ideal natural classification.

MORPHOLOGICAL CHARACTERS.

In a review of the morphological characters it is found that the tarsus and tibia are of special value in the classification of the superfamily; the head, pronotum, elytra, and third joint of the tarsus for the family; the head, tarsi, pronotum, elytra, anterior coxæ, abdominal sternite, and pygidium for the subfamily: the antennæ, eyes, pronotum, elytra, tarsi, tibiæ, body, abdominal sternites, anterior coxæ, and mouthparts for the genus, and for the species there is such a wide range of characters of varying, and sometimes reverse, value in different genera that they can not be specified except for limited groups. However, the size, form, color, vestiture, and sculpture of the body, the front of the head, elytral declivity, etc., are in general among the most important bearers of specific characters.

In the digestive system the masticatory plates of the proventriculus appear to be of special taxonomic value when applied to subfamilies, genera, and species.

In the reproductive organs of the male there is a very wide range of variation in the primary and secondary elements of the posterior or chitinized section, but with a few exceptions their taxonomic value appears to be restricted to major and minor divisions of the genus and especially to the separation of the species. In the anterior section of the organs the length of the ductus ejaculatorius and the form of the testes, seminal vesicles, vas deferens, and mucus glands appear to represent the principal taxonomic elements, and they are of varying value as applied to major and minor groups.

The female reproductive organs, like the proventriculus, appear to possess a number of taxonomic characters of family, subfamily, and generic value, such as the presence or absence of the cement glands and their varying characters and the presence and character of the spermatheca with its seminal duct.

In the secondary sexual characters we find a few which are peculiar to a genus or to groups of allied genera, but in general their principal value appears to be in distinguishing the species.

In the pupæ it is found that the head and the tergal, lateral, pleural, caudal, and femoral spines appear to be the most important taxonomic elements.

In the larvæ there is a wide range of variation in the form of the body and in some of the primary elements of the head and posterior

abdominal segments, spiracles, etc., which are of value in separating the families, but the majority of these characters are of greatest value in connection with the genera and species.

The egg and embryo doubtless bear some important characters, but they have not been sufficiently studied by the writer to justify their discussion in this connection.

PHYSIOLOGICAL CHARACTERISTICS.

A review of the evidence relating to the physiological characteristics shows that the feeding, breeding, flight, and social habits, the galleries, larval mines, host plants, the species of plant, the part of the plant occupied, conditions of the plant, restricted or wide range of host relations, and features in geographical distribution have something to contribute in facts and evidence of more or less taxonomic importance.

CORRELATION OF MORPHOLOGICAL AND PHYSIOLOGICAL ELEMENTS.

In order to arrive at satisfactory conclusions in regard to the proper correlation of the mass of taxonomic data mentioned in the foregoing review one must have a far more comprehensive and first-hand knowledge of the subject as applied to the species of the world than is possessed by any investigator at the present time. Therefore it is the object of the writer to call attention to the need of further investigation of this broader principle of zoological taxonomy rather than to attempt to draw conclusions. It is evident, however, that at some future time the essential facts will be correlated into a system which will not only indicate true natural relations but perhaps give a better clue to the action of natural laws and a better interpretation of the fundamental principles involved in the evolution of life in general.

In order to arrive at sound conclusions the whole subject must be investigated without prejudice for or against any theory as to phylogenetic origin of the organism, or as to the primitive or recent character of an organ or element. The problem must be attacked with the view of locating the more important or essential facts relating to the distinguishing characters and characteristics as applied to the species and their various aggregations into genera, subfamilies, and families and the major and minor divisions of each. In other words, a given group of organisms should be studied in all of its morphological and physiological aspects with the view of locating, by the process of elimination, the elements of primary importance until one or more characters in each of the principal morphological and physiological groups of taxonomic elements are found to correlate in the formation of a harmonious taxonomic compound.

It has been shown in the foregoing pages that a classification based on any limited set of external or internal elements of the adult body,

such as those found in the proventriculus or in the male or female organs, will suggest a phylogenetic system, but when it is found that each system differs from the other to such an extent that the same genus or species will occupy a radically different position in the different systems it is perfectly plain that the true taxonomic value of the elements has not been correctly interpreted or applied. On the other hand, it is equally plain that if characters can be found in all or a majority of the groups of external and internal elements which point in the same direction, we may safely assume that we have more nearly approached the true principle involved and the ideal classification.

Examples of an attempt by the writer to correlate and harmonize the various morphological and physiological elements will be found in the synoptic tables of *Dendroctonus*, Part I of this bulletin, and of *Pissodes* in Technical Series 20, Part I.

PARALLEL MODIFICATIONS.

Parallel modification in morphological and physiological elements is without doubt an important factor to be considered in taxonomy. It is evident from a comparative study of the various systems of classification that the failure of taxonomists fully to realize its importance has in many cases led to wrong conclusions. It has been shown in the foregoing discussion that there are a great many examples of parallel characters and characteristics in widely separated species and genera and that if they are not recognized and properly interpreted as such by the taxonomist, radically wrong positions will be assigned to many species and genera.

REVERSALS.

The reversal of characters and characteristics in different species of the same genus or in different genera and larger groups is another important fact to be kept in mind, especially as related to secondary sexual characters. Therefore it is never safe to conclude that because a given character or a group of characters is of special value in distinguishing one group, genus, species, or sex, it will hold in all cases. There have been numerous examples of wrong determination of the sexes from a failure to recognize this principle, as has been pointed out by the writer (Hopkins, 1894, pp. 274–280) and Blandford (1895, pp. 83–86). As has been shown on preceding pages, reversals are also found in specific, generic, and group characters, even to the subdivision of the superfamily, where we find a most striking example in the reversal of the apical spine or process of the anterior tibia from the inner to the outer angle.

PROGRESSIVE MODIFICATIONS.

The discontinuous yet more or less progressive change or variation in the modification of morphological and physiological elements along definite lines within the minor to major groups is very evident in every group. The more this subject is studied the more we are convinced that there are certain important facts involved in this principle that have not been satisfactorily explained by any theory of the processes of evolution. The recognition and application in taxonomy of those unexplained features does not, however, necessarily require the acceptance or rejection of any theory of orthogenesis or phylogenesis. It is only necessary to correlate them with other more easily explained elements of distinction or to utilize them as guides to the position a species or group should occupy in a given series.

Examples of Progressive Modification.

The examples of progressive modification in morphological characters and physiological characteristics which have been noted by the writer in the scolytoid beetles may be summarized as follows:

Morphological characters.

Body small to large.

Body slender to stout.

Body with scales to hairs, to glabrous.

Head concealed to exposed.

Head short and broad to narrow and subrostrate.

Head with front convex, glabrous, to concave and pubescent or fringed.

Head with eyes oblong, elliptical and not emarginate, to short, oval, and deeply emarginate or divided.

Antennal joints of funicle increasing in number to the limit of seven.

Antennal joints of club decreasing in number through fusion or disappearance of sutures.

Prothorax long and narrow to short and broad.

Prothorax with sides not margined to margined, or not emarginate to emarginate.

Prothoracic pleurum convex to flat and concave.

Tarsi with third joint simple to emarginate and bilobed.

Tarsi with first joint short to long.

Elytral declivity convex and smooth to rugose and armed; retuse to concave, with the margin unarmed to strongly armed.

Sexes of unequal size and the males rare to equal size and the males common.

Secondary sexual characters obscure to prominent.

Galleries.

Simple cavities in decaying bark and wood, to complex designs and regular forms of egg galleries and larval mines.

Excavated in bark to excavated in wood, seeds, etc.

Social habits.

Unorganized polygamy to organized polygamy, to highly organized monogamy.

Independent larvæ, procuring their own food, to dependent larvæ, with the food provided by the maternal parent.

STATISTICAL TAXONOMY.

The subject of statistical taxonomy has received considerable attention by the writer and an attempt has been made (Hopkins, 1911, pp. 28–30, Pl. II) to show its successful application in the genus *Pissodes*. The detail and accuracy required for this method and the difficulty of determining a specific and taxonomic formula are so great, however, as to be rather trying on the patience of the investigator. Therefore it is the opinion of the writer that it should not be resorted to except in cases in which other methods fail to give satisfactory results and then only when the elements to be included are of such a nature as to be readily available for the mathematical determination of relative proportions. There is in this, as in many subjects relating to taxonomy, a need of a more comprehensive investigation in order that the most reliable basis for conclusions may be reached.

THE SPECIES.

Reference has been made (Part I, p. 66) to the writer's views on specific distinction and the range and limits of specific variation. In addition it may be said that no species can be established beyond dispute without a knowledge of both the morphological and physiological elements of distinction. This does not, however, preclude the recognition and naming of imperfectly defined and poorly represented species and of retaining them as long as they can be readily distinguished from other allied forms. Such names and definitions serve as a basis for study until it is more definitely shown whether or not the forms are worthy of permanent specific distinction. There is necessarily a wide range in the relative prominence of the distinguishing characters as between a species which is the only representative of a genus and subfamily and one of a group of closely allied species. It is found, however, that for the purpose of systematic and economic investigation the isolated species may be of no more value for study and may contribute no more to the advancement of knowledge than the one which is with difficulty separated from its congeners.

Since we now insist upon a single specimen as the author's designation of the type of a described species it is deemed by the writer to be perfectly proper to base the description of a new species on a single specimen, provided the author of the description is sufficiently familiar with the previously described allied species and genera to enable him to recognize the characters and characteristics which are of real specific importance.

VARIETIES, RACES, ETC.

There is in all species a greater or lesser range of variation from the type, and often some groups of individuals may be so different as to indicate a distinct variety or race. If such variant forms are

found intermingled with the broods of the typical forms and the characters are not sufficiently constant to distinguish them as separate species they should simply be considered as coming within the range of specific variation, but in the writer's opinion these varieties should not be distinguished by a trinomial.

In some genera and species the sexes may so differ in whole groups of characters as to indicate, in some cases, different genera. But there is always some character or set of characters common to both sexes which would point to the same species even if they were not found associated in the same brood.

There is evidence that in some of the species of *Xyleborus* and allied genera in the Cryphalinæ there may be occasional individuals which represent a degenerate form or a caste in the social relations of a brood or colony, with uniform but radically different characters from those of either sex, and that on account of the radical differences which separate them from the species with which they have been found they have heretofore been recognized as good species. *Xyleborus planicollis* Zimm. may be such an odd member of the *Xyleborus inermis* colony and *Xyleborus viduus* Eichh. an odd type of the *Xyleborus fuscatus* colony, but further observations will be needed to settle the question. If this should be true in these cases it may hold with isolated cases in other social species, like those of *Hypothenemus, Stephanoderes, Dryocœtes*, etc.

THE GENUS.

There is more latitude, perhaps, for the selection of distinguishing characters of the genera than there is for the species, but the same principle applies. There must be some single character or group of characters common to a group of allied species which will serve to distinguish the group readily from all other allied groups. The range of departure or variation from the type of the genus is restricted in some genera, but in other genera with many species there may be a very wide range, so that the species will fall in distinct divisions and subdivisions, which are designated by some authors as subgenera.

Unfortunately there is a wide range in the opinions of different authors as to the limits of a genus. Some go to the extreme in restricting it to closely allied species while others go to the opposite extreme (Hagedorn, 1910) and include a large number of genera or so-called subgenera. It is plain to the writer that of the two extremes the latter is the more objectionable because it will certainly contribute more than the former toward retarding than advancing knowledge. The writer believes that there is a middle ground on which systematists should endeavor to get together in order that there may be more uniformity in the conception and definition of the genus.

NOMENCLATURE.

Nomenclature, as applied to taxonomy, is a subject on which there are wide differences of opinion, and it is evident that until there is more uniformity there will be continued contributions to the confusion of knowledge along with those which contribute to its advancement.

It seems to the writer that the subject of designating by name varieties, forms, races, subspecies, and subgenera should demand the special attention of systematists with the view of coming to an understanding as to the limiting of such names to the more definite concepts, as those of the species or genus. It would seem that if we should limit the names to the species, genera, subfamilies, families, and superfamilies within an order and designate the major and minor divisions of each as divisions (I, II), subdivisions (A, B, C, D), sections (a1, a2, etc.), subsections (b1, b2, etc.), series (c1, c2, etc.), and subseries (e1, e2, etc.), it would be in the line of progress toward a consistent, practical, and uniform method of expressing the varying ranks as interpreted by different authors. It would avoid, at the same time, the use of names for divisions and subdivisions which have different meanings in the systems proposed by different authors and prevent the accumulation of obsolete names with every change or important advance in the classification.

In the systematic treatment of the scolytoid beetles the writer fails to see the need of recognizing subspecies or subgenera. The species and the genus are the two most important biological concepts on which to base both systematic and economic investigations. They serve, also, as the most important units on which to base a classification. Therefore the writer holds that the individual represents a species and that a species represents a genus; hence the introduction of the trinomial for a subspecies and the naming of a subgenus are unnecessary. Moreover, he believes that a general practice of giving names to such divisions of these taxonomic units will ultimately lead to endless confusion and retard rather than advance the spirit of research and the acquisition of knowledge. At best the designation of the species and the genus to which a given individual should be referred is an arbitrary interpretation of a concept. Therefore, when an author designates an individual or a group of individuals as representing a subspecies, or a group of species as representing a subgenus, it involves the assumption that the concept is a fact and that he has sufficient knowledge of this fact to enable him to analyze it into component categories the relations of which are so definitely determined as to justify the subordination of one part to another.

There is such a wide range for the interpretation of specific and generic distinctions and such a vast difference in the relative rank of such distinctions, between isolated survivors of highly specialized and

ancient groups and common, closely allied, and variable forms, that the difference between two species in one genus may be equivalent to or greater than that between two allied genera. In a like manner the difference between two genera may be almost equivalent in rank to that between two allied subfamilies. Therefore the fact that a given group of individuals or a group of species appears to represent a position of lower rank than that of an allied species or genus is not sufficient reason that it should be designated as a subspecies or subgenus. In other words, it is the writer's opinion that if a group of individuals is sufficiently distinct from allied groups to justify its designation by a name, it should be recognized as a species; and if, on the other hand, the group is connected with allied forms by such a number of intermediate forms as to render its specific distinction doubtful, it should be included with other variable types under a species name, and that the same principle should hold in regard to the genus.

All of the purposes served by the subspecific designation can be served just as well, if not better, by classifying the individuals of a species into major and minor divisions, sections, etc., and letting these represent the same conception as that represented by the named subspecies, and on the same principle the divisions and subdivisions of a genus will serve the same purpose as if designated by names.

TYPES OF GENERA.

Difference of opinion among systematists who have worked on the scolytoid beetles, guided as they have been by different rules and conceptions as to what constitutes a valid genus, has led to much uncertainty and confusion as to some of the older names for the genera of our common species. Therefore it seems necessary that the author should present the evidence which appears to him to be conclusive in regard to the generic names and the synonymy of *Scolytus*, *Ips*, *Tomicus*, *Cryphalus*, *Hypothenemus*, etc.

Genus SCOLYTUS Geoffroy.

It has seemed to the writer that there is not sufficient reason or authority for the suppression of the name *Scolytus* as proposed and clearly defined by Geoffroy (1762, p. 309). The single "species" of the "genus" recognized by him was at the same time (p. 310) indicated by a number, the genus name (*Scolytus*), and a reference to a figure (Vol. I, pl. 5, fig. 5), and the characters were more clearly defined in a description.

Müller (1764, p. xiv) recognized the genus *Scolytus* Geoff. and referred to the original description and figures.

Schaeffer (1766, Tab. CXII, figs. 1, 2, 3, 4) redescribed the genus *Scolytus* and described and figured the species indicated by Geoffroy, but did not name it.

The fact that specimens were collected in the wood indicates that the food habits are similar to those of *Crossotarsus lecontei*, found in the same log.

The pupa is peculiar in the absence of caudal spines, the presence of tergal and pleural hairs instead of tubercles, and the length of the wing-pads, which extend to the apex of the abdomen.

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(See Pl. IX.)

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  B. Anterior tibia with prominent process on the outer apical angle.
    a1. Anterior tibia without prominent rugosities on ventral area. Family Scolytidæ.
    a2. Anterior tibia with prominent rugosities on ventral area. Family Scolytoplatypodidæ.

II. Anterior tarsi with joint 1 longer than 2, 3, and 4 together.
  C. Anterior tibia with prominent apical process and with rugosities on the ventral area..... Family Platypodidæ.

Family IPIDÆ.

KEY TO THE SUBFAMILIES.

(See Pls. X, XI, XIII, XIV.)

I. Pronotum with anterior dorsal area commonly rugose; head concealed from above; anterior tarsi with joint 3 simple.
  A. Abdominal sternites 5–7 not strongly ascending.
    a1. Anterior tibia broader toward apex or serrate on outer margin.
      b1. Abdominal sternite 7 with posterior margin always rounded. 1. Subfamily Cryphalinæ.
      b2. Abdominal sternite 7 with posterior margin rarely rounded.
        c1. Pronotum and elytra clothed with scales or hairs, very rarely glabrous..... 2. Subfamily Ipinæ.
        c2. Pronotum and elytra without scales, commonly glabrous or sparsely pubescent..... 3. Subfamily Corthylinæ.
    a2. Anterior tibia not distinctly broader toward apex or not serrate on outer margin.
      b3. Anterior tibia not strongly narrowed toward apex, apical tooth stout; antennal club compressed; elytra with scales. 4. Subfamily Micracinæ.
      b4. Anterior tibia strongly narrowed toward apex, apical tooth small; antennal club thickened at base, with anterior face obliquely truncate; elytra with hairs..... 5. Subfamily Webbinæ.
  B. Abdominal sternites 5–7 strongly ascending; tibia broadly compressed, outer margin serrate..... 6. Subfamily Xyloctoninæ.

ancient groups and common, closely allied, and variable forms, that the difference between two species in one genus may be equivalent to or greater than that between two allied genera. In a like manner the difference between two genera may be almost equivalent in rank to that between two allied subfamilies. Therefore the fact that a given group of individuals or a group of species appears to represent a position of lower rank than that of an allied species or genus is not sufficient reason that it should be designated as a subspecies or subgenus. In other words, it is the writer's opinion that if a group of individuals is sufficiently distinct from allied groups to justify its designation by a name, it should be recognized as a species; and if, on the other hand, the group is connected with allied forms by such a number of intermediate forms as to render its specific distinction doubtful, it should be included with other variable types under a species name, and that the same principle should hold in regard to the genus.

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Linnæus (1767) failed to mention the genus or to refer to Geoffroy, Müller, or Schaeffer.

Fabricius (1775, p. 59) recognized the species described by Geoffroy and redescribed it under the name *Bostrichus scolytus*, with the citation "Geoff. Ins. 1–310, [No.] 1, Tab. 5, fig. 5, Mal." Thus Fabricius recognized the species indicated by Geoffroy on page 310, but did not refer it to the genus described on page 309 under the name *Scolytus* because he (Fabricius) evidently considered it synonymous with *Bostrichus*. Consequently, the name proposed by Geoffroy for the genus should stand with *Bostrichus scolytus* (Fab.) as the type.

Sulzer (1776, Th. 1, p. 21; Th. II, Tab. II, f. 13k), under the name *Dermestes scolytus*, described and figured the species indicated by Schaeffer, 1766.

Müller (1776, p. 57) published a description under the name *Scolytus punctatus* but referred it doubtfully to Geoffroy's figures.

Goeze (1777, p. 143), under the name "*Dermestes scolytus* Geoffroi," cited *Bostrichus scolytus* Fab. (1775), *Scolytus* Geoff. (1762), and *Scolytus punctatus* Müll. (1776). Goeze evidently did not mention "Geoffroi" as a specific name but merely to indicate that Geoffroy was the author of or authority for the name *Scolytus*.

Linnæus (1788, 1793, p. 1602) recognized *Bostrichus scolytus* Fab. and cited Fabricius, 1787, Geoffroy, 1762, Sulzer, 1776, and Schaeffer, 1766.

Herbst (1793, p. 124) described the genus *Eccoptogaster* with *Bostrichus scolytus* Fab. as the type.

Olivier (1795, No. 78, p. 5, Pl. I, fig. 4 a, b, c) adopted the name *Scolytus* for the genus and cited Geoffroy, 1762, and Fabricius, 1775, but substituted for the species the name *destructor* in the place of *Scolytus* Fab., evidently concluding, as other contemporary writers did, that the generic and specific names could not be the same. In fact this opinion evidently influenced the action of Fabricius, Müller, Herbst, and others.

Curtis (1824, p. 43) designated the type of the genus *Scolytus* as *Bostrichus scolytus* Fab.

Genus IPS De Geer.

There appears to be no room for doubt that the genus *Ips* of De Geer (1775, p. 190), with *Dermestes typographus* Linn., 1758, as the type, has priority over *Ips* of Fabricius (1776, p. 23).

Genus TOMICUS Latreille.

Latreille (1802, p. 203) described the genus *Tomicus* with *Hylesinus piniperda* Fab. (1801, p. 392) as the type, but *H. piniperda* of Fabricius is, as cited by him (1801, p. 392), the same as *Bostrichus piniperda* (L.) Fab. (1775, p. 60; 1792, p. 367) and *Dermestes pini-*

perda Linn. (1758, p. 355 and 1767, p. 563). Therefore it appears that the name *Tomicus* should stand, with *Hylesinus piniperda* (L.) Fab. as the type. The slight difference in the description by Fabricius of the insect he identified as Linnæus's species does not warrant the conclusion that it was different, because the species has the characters mentioned.

The species **piniperda** L.

piniperda L., *Dermestes* Linnæus, 1758, p. 355; 1761, p. 143; 1767, p. 363.
piniperda L., *Bostrichus* Fabricius, 1775, p. 60; 1792, p. 367.
piniperda L., *Hylesinus* Fabricius, 1801, p. 392.
piniperda L., *Tomicus* Latreille, 1802, p. 203. (Type of genus.)
piniperda L., *Blastophagus* Eichhoff, 1864, p. 25. (Type of genus.)
piniperda L., *Myelophilus* Eichhoff, 1878, p. 400. (Type of genus.)

Genus HYLASTES Erichson.

Erichson (1836, p. 48) described the genus *Hylastes* to include *Bostrichus ater* Paykull, *Bostrichus angustatus* Herbst, etc., stating that *Bostrichus ater* Fab. was not a scolytid. Therefore, since *Bostrichus ater* Paykull is a good species, it stands as the type of the genus *Hylastes* Erichson, as designated by Thomson, 1859, p. 146.

Genus CRYPHALUS Erichson.

Erichson (1836, p. 61) described the genus *Cryphalus* to include *Apate tiliæ* Panz., *Apate fagi* Fab., and *Bostrichus asperatus* Gyll. Thomson (1859, p. 146) designated (*Bostrichus*) *Cryphalus asperatus* Gyll. as the type and (p. 147) referred *Cryphalus tiliæ* Panz. to his monobasic subgenus *Ernoporus* and (1865, p. 360) *Cryphalus fagi* Fab. to *Ernoporus*.

Hypothenemus Westw., 1834, p. 34; *Ernoporus* Thom., 1859, p. 147; *Trypophlœus* Fairm., 1868, p. 105; *Stephanoderes* Eichh., 1871, p. 132, and *Cryphaloides* Form., 1908, p. 91, are all sufficiently distinct from *Cryphalus* Erich. and from one another to stand as separate and distinct genera; therefore they should not, in the opinion of the writer, be considered as subgenera of *Cryphalus*.

Genus HYPOTHENEMUS Westwood.

Westwood (1834, pp. 34, 36, Pl. VII, fig. 1a to h) described the genus *Hypothenemus* with *eruditus* Westw. as the only species and mentioned and illustrated a three-jointed funicle of the antenna as one of the distinguishing characters.

Duvall (1868, p. 105, pl. 33, fig. 161) examined specimens from the type series and redescribed and figured the species, and referred to the funicle as having but three joints.

Eichhoff (1879, p. 165) referred the genus *Hypothenemus* Westw., and species *eruditus* Westw. to synonymy under *Stephanoderes*

ariccæ (Hornung, 1842, p. 117 [not 115]) because he found that certain species previously referred to *Hypothenemus* had five joints in the funicle of the antenna instead of three, as designated by Westwood.

Fauvel (1884, p. 315) examined specimens of *H. eruditus* Westw. from the type series and compared them with examples of *Bostrichus boieldieui* Perroud, 1864, p. 188, and *B. ariccæ* Hornung, 1842, p. 117, identified by Eichhoff, and concluded that all three were identical, and that *Homœocryphalus* Lind., 1876, p. 168, as represented by *Stephanoderes ehlersi* Eichh., was identical with *Hypothenemus* Westw.

Newberry (1910, p. 83) determined that the funicle had four joints.

Through the kindness of Prof. Poulton, the writer had the opportunity of examining a specimen of *H. eruditus* Westw. from the type series, and the funicle was found to be four-jointed. It is not improbable, however, that the antenna examined by Westwood was from a male, which, in this genus, is smaller than the female and has but three joints in the funicle. Therefore there can be no doubt as to the validity of the genus *Hypothenemus* Westw. as distinguished from the genus *Stephanoderes* Eichh., which has a five-jointed funicle.

Genus POLYGRAPHUS Erichson.

Erichson (1836, p. 57–58) described the genus *Polygraphus*, citing *Dermestes polygraphus* L. (1758, p. 355) as synonymous with *P. pubescens* Fab. (1792, p. 368); but since *P. polygraphus* L. has priority, the genus stands with *Dermestes polygraphus* L. as the type.

Genus LEPISOMUS Kirby.

Kirby (1837, p. 193) described *Lepisomus* as a subgenus of *Apate* Fab., including three species, one of which, *Apate* (*Lepisomus*) *nigriceps*, has been referred to synonymy (Lec., 1868, p. 169) while *Apate* (*Lepisomus*) *brevicornis* is not recognizable, probably a synonym. Therefore *Apate* (*Lepisomus*) *rufipennis* Kirby is the type of the genus *Lepisomus*, which, on account of the six-jointed funicle, is a good genus. For the same reason *Polygraphus grandiclava* Thom. (1886, p. 62) must also be referred to this genus.

DESCRIPTION OF A NEW GENUS AND SPECIES.

WEBBIA n. gen.[a]

Antennal funicle four-jointed, the fourth broad; club narrowed from middle to base, broader than long, with one sinuate chitinous suture on the obliquely truncate anterior face, the posterior face

[a] This genus and species is described here in order that the subfamily may be included in the classification.

without sutures; eyes oblong, elliptical, deeply emarginate; anterior tibia strongly narrowed to apex, with submarginate row of closely placed teeth on the ventral side; elytral declivity with many closely placed marginal teeth; lateral margin of pronotum acute, anterior margin without serrations. Type of genus, *Webbia dipterocarpi* new species.

This genus is named for Mr. J. L. Webb on account of the large number of scolytoid beetles collected by him during his brief employment in the Philippine service.

Webbia dipterocarpi n. sp.

Length, female type, 3.1 mm. Subelongate; pronotum and all but the declivity of the elytra light ferruginous, the declivity black. Pronotum with anterior area swollen, opaque, nearly smooth; apex steep, subtruncate, and finely rugose; median and posterior areas smooth, subopaque, and very finely punctured. Front moderately narrow, subconvex, opaque, with fine median line. Elytra to near declivity smooth, shining, with fine, closely placed, and confused punctures with no trace of striæ, narrow, and near vertex slightly swollen, densely opaque, nearly black; declivity steep, flat, opaque; interspace 1 elevated, smooth; interspaces 2 and 3 each with straight rows of granules; margin from vertex to apex armed each side with 10 closely placed serrations or teeth, becoming slightly larger toward apex. These teeth evidently represent the 10 interspaces of the normal elytra. Near Pagbilao, Philippine Islands, in wood of dead log of *Dipterocarpus grandiflorus* Blco., August 7, 1903. J. L. Webb, collector. Under his number 94c.

Type.—Cat. No. 7406, U. S. National Museum.

Length, male type, 2.6 mm. Subelongate; pronotum slightly broader than elytra which are narrowed toward declivity, light ferruginous throughout. Head narrow, shining, with deep epistomal impression and a slight posterior impression. Pronotum opaque, finely rugose throughout, with distinct median impressed shining line to anterior declivity which is steep and strongly retuse to anterior margin, sides slightly narrowed from anterior angles to base, lateral margins subobtuse; elytra with sides slightly narrowed toward declivity, shining, punctured as in female but with striæ evident and faintly impressed; declivity steep, flat, opaque, rugose, but without elevated interspaces, margin with but seven marginal teeth, coarser toward vertex and arranged in groups of 3–2–2. In a lateral aspect the dorsal line forms a broad curve from the mandibles to the apex of the abdomen. From same colony as the female.

The smaller size and general appearance of the male suggests affinities with the *Xyleborus* group but it is radically different in all of the more important characters.

The fact that specimens were collected in the wood indicates that the food habits are similar to those of *Crossotarsus lecontei*, found in the same log.

The pupa is peculiar in the absence of caudal spines, the presence of tergal and pleural hairs instead of tubercles, and the length of the wing-pads, which extend to the apex of the abdomen.

The larva, as shown by a dried specimen, appears to have the posterior part of the body stouter, then narrowed toward the apex of the abdomen.

PRELIMINARY CLASSIFICATION OF THE SUPERFAMILY SCOLYTOIDEA.

KEY TO THE FAMILIES.

(See Pl. IX.)

I. Anterior tarsi with joint 1 shorter than 2, 3, and 4 together.
  A. Anterior tibia without prominent process on the outer apical angle. Family Ipidæ.
  B. Anterior tibia with prominent process on the outer apical angle.
    a1. Anterior tibia without prominent rugosities on ventral area. Family Scolytidæ.
    a2. Anterior tibia with prominent rugosities on ventral area. Family Scolytoplatypodidæ.

II. Anterior tarsi with joint 1 longer than 2, 3, and 4 together.
  C. Anterior tibia with prominent apical process and with rugosities on the ventral area ..... Family Platypodidæ.

Family IPIDÆ.

KEY TO THE SUBFAMILIES.

(See Pls. X, XI, XIII, XIV.)

I. Pronotum with anterior dorsal area commonly rugose; head concealed from above; anterior tarsi with joint 3 simple.
  A. Abdominal sternites 5–7 not strongly ascending.
    a1. Anterior tibia broader toward apex or serrate on outer margin.
      b1. Abdominal sternite 7 with posterior margin always rounded. 1. Subfamily Cryphalinæ.
      b2. Abdominal sternite 7 with posterior margin rarely rounded.
        c1. Pronotum and elytra clothed with scales or hairs, very rarely glabrous ..... 2. Subfamily Ipinæ.
        c2. Pronotum and elytra without scales, commonly glabrous or sparsely pubescent ..... 3. Subfamily Corthylinæ.
    a2. Anterior tibia not distinctly broader toward apex or not serrate on outer margin.
      b3. Anterior tibia not strongly narrowed toward apex, apical tooth stout; antennal club compressed; elytra with scales. 4. Subfamily Micracinæ.
      b4. Anterior tibia strongly narrowed toward apex, apical tooth small; antennal club thickened at base, with anterior face obliquely truncate; elytra with hairs ..... 5. Subfamily Webbinæ.
  B. Abdominal sternites 5–7 strongly ascending; tibia broadly compressed, outer margin serrate ..... 6. Subfamily Xyloctoninæ.

II. Pronotum with anterior dorsal area commonly smooth; head exposed or rarely concealed from above; tarsi with joint 3 simple or bilobed.

C. Antennal club subglobose, compressed to laminate, never conical.

a3. Body slender to moderately stout; pronotum longer than broad or not broader than long ..... 7. Subfamily Crypturginæ.

a4. Body stout; pronotum always broader than long.

8. Subfamily Phlœotribinæ.

D. Antennal club usually conical, rarely compressed ..9. Subfamily Hylesininæ.

10. Subfamily Phlœoborinæ.

Family SCOLYTIDÆ.

KEY TO THE SUBFAMILIES.

(See Pls. XII, XV, XVI.)

I. Pronotum constricted toward the middle; anterior tarsi with joint 3 simple.

11. Subfamily Coptonotinæ.

II. Pronotum not constricted toward the middle; anterior tarsi with joint 3 simple or bilobed.

A. Anterior tibia with small tooth on inner apical angle extending beyond the tarsal insertion; tibia with at least one tooth on the outer margin, in addition to the apical one.

a1. Eyes not divided; tibia with outer margin armed.

b1. Pronotum with transverse rugosities on anterior area.

12. Subfamily Hexacolinæ.

b2. Pronotum without transverse rugosities on anterior area.

13. Subfamily Bothrosterninæ.

a2. Eyes divided; tibia with outer margin unarmed.[a]

14. Subfamily Hyorrhynchinæ.

B. Anterior tibia with small tooth on inner apical angle not extending beyond the tarsal insertion.

a3. Abdominal sternum convex throughout; antennal scape not very short.

15. Subfamily Camptocerinæ.

a4. Abdominal sternum not convex throughout; antennal scape very short.

16. Subfamily Scolytinæ.

Family SCOLYTOPLATYPODIDÆ.

(See Pls. XII, XVI.)

Anterior tibia with prominent lateral process at outer angle; third tarsal joint simple ..... 17. Subfamily Scolytoplatypodinæ.

Family PLATYPODIDÆ.

KEY TO THE SUBFAMILIES.

(See Pls. XII, XVI.)

I. Third tarsal joint simple ..... 18. Subfamily Platypodinæ.

II. Third tarsal joint bilobed ..... 19. Subfamily Genyocerinæ.

20. Subfamily Chapuisinæ.

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[a] Uncertain from description whether or not inner angle of anterior tibia is produced beyond the tarsal insertion.

POSITION OF THE PRINCIPAL DESCRIBED GENERA IN THE PRELIMINARY CLASSIFICATION.

Family Ipidæ.
- Subfamily Cryphalinæ.
  - *Cosmoderes* Eichh.
  - *Cryphalomorphus* Schauff.
  - *Hypothenemus* Westw.
  - *Stephanoderes* Eichh.
  - *Ernoporus* Thoms.
  - *Trypophlœus* Fairm.
  - *Cryphalops* Reitt.
  - *Cryphaloides* Form.
  - *Cryptarthrum* Blndfd.
  - *Cryphalus* Erich.
  - *Eidophelus* Eichh.
  - *Kyrtogenius* Stroh.
  - *Lepicerus* Eichh.
  - *Lymantor* Løv.
  - *Dendroterus* Blndfd.
  - *Xylocleptes* Ferr.
  - *Taphrorychus* Eichh.
  - *Thamnurgus* Eichh.
  - *Coccotrypes* Eichh.
  - *Ozopemon* Haged.
  - *Dryocœtes* Eichh.
  - *Xyleborus* Eichh.
  - *Anisandrus* Ferr.
  - *Eccoptopterus* Motsch.
  - *Cnestus* Sampson.
- Subfamily Ipinæ.
  - *Pityophthorus* Eichh.
  - *Olonthogaster* Motsch.
  - *Acanthotomicus* Blndfd.
  - *Pityogenes* Bedel.
  - *Ips* De Geer.
- Subfamily Corthylinæ.
  - *Metacorthylus* Blndfd.
  - *Monarthrum* Kirsch.
  - *Cosmocorynus* Ferr.
  - *Phthorius* Eichh.
  - *Anchonocerus* Eichh.
  - *Glochinocerus* Blndfd.
  - *Tricolus* Blndfd.
  - *Amphicranus* Erich.
  - *Steganocranus* Eichh.
  - *Corthylus* Erich.
  - *Brachyspartus* Ferr.
  - *Gnathotrichus* Eichh.
  - *Premnobius* Eichh.
  - *Xyloterus* Erich.
- Subfamily Micracinæ.
  - *Pœcilips* Schauf.
  - *Thysanoes* Lec.

Family Ipidæ—Continued.
- Subfamily Micracinæ—Continued.
  - *Micracis* Lec.
  - *Hylocurus* Eichh.
  - *Styracopterus* Blndfd.
  - *Liparthrum* Woll.
  - *Dacryostactus* Schauff.
  - *Hypoborus* Erich.
  - *Glochiphorus* Stroh.
  - *Cactopinus* Schwarz.
- Subfamily Webbinæ.
  - *Webbia* n. gen.
- Subfamily Xyloctoninæ.
  - *Scolytogenes* Eichh.
  - *Scolytonomus* Blndfd.
  - *Scolytodes* Ferr.
  - *Xyloctonus* Eichh.
  - *Gtonoxylon* Haged.
- Subfamily Crypturginæ.
  - *Aphanarthrum* Woll.
  - *Triotemnus* Woll.
  - *Crypturgus* Eichh.
  - *Cisurgus* Reitt.
  - *Dolurgus* Eichh.
  - *Dendroctonus* Erich.
- Subfamily Phlœotribinæ.
  - *Phlœophthorus* Woll.
  - *Eulytocerus* Blndfd.
  - *Phlœotribus* Latr.
  - *Dryotomus* Chap.
  - *Renocis* Casey.
  - *Chætophlœus* Lec.
  - *Chramesus* Lec.
  - *Chortastus* Schauff.
  - *Carphoborus* Eichh.
  - *Cladoctonus* Stroh.
  - *Lissoclastus* Schauf.
  - *Tiarophorus* Schrein.
  - *Phrixosoma* Blndfd.
  - *Lepisomus* Kirby.
  - *Polygraphus* Erich.
  - *Spongotarsus* Haged.
- Subfamily Hylesininæ.
  - *Xylechinus* Chap.
  - *Kissophagus* Chap.
  - *Hylurgus* Latr.
  - *Pachycotes* Sharp.
  - *Tomicus* Latr. (*Myelophilus* Eichh.)
  - *Hylastinus* Bedel.
  - *Scierus* Lec.

Family Ipidæ—Continued.
Subfamily Hylesininæ—Continued.
Hylesinus Fab.
Pteliobius Bedel.
Dendrosinus Chap.
Acanthophorus Stroh.
Hylurgops Lec.
Hylastes Erich.
Subfamily Phlœoborinæ.
Phlœotrupes Erich.
Phlœoborus Erich.
Dactylipalpus Chap.
Family Scolytidæ.
Subfamily Coptonotinæ.
Craniodicticus Blndfd.
Microborus Blndfd.
Coptonotus Chap.
Subfamily Hexacolinæ.
Erineophilus Hopk.
Hexacolus Erich.
Epomadius Blndfd.
Problechilus Eichh.
Aricerus Blndfd.
Pycnarthrum Eichh.
Prionoceles Blndfd.
Rhopalopselion Haged.
Strombophorus Haged.
Sphærotrypes Blndfd.
Diamerus Erich.
Bothryperus Haged.
Subfamily Bothrosterninæ.
Pagiocerus Eichh.
Cnesinus Lec.
Meringopalpus Haged.

Family Scolytidæ—Continued.
Subfamily Bothrosterninæ—Contd.
Eupagiocerus Blndfd.
Bothrosternus Eichh.
Subfamily Camptocerinæ.
Ceratolepis Chap.
Cnemonys Eichh.
Camptocerus Dej.
Loganius Chap.
Subfamily Scolytinæ.
Scolytopsis Blndfd.
Scolytus Geoff.
Family Scolytoplatypodidæ.
Subfamily Scolytoplatypodinæ.
Scolytoplatypus Schauff.
Spongocerus Blndfd.
Tæniocerus Blndfd.
Family Platypodidæ.
Subfamily Platypodinæ.
Spathidiceres Chap.
Periommatus Chap.
Tesserocerus Saund.
Symmerus Chap.
Cenocephalus Chap.
Mitosoma Chap.
Diapus Chap.
Cylindropalpus Stroh.
Platypus Herbst.
Crossotarsus Chap.
Subfamily Genyocerinæ.
Genyocerus Motsch.
Subfamily Chapuisinæ.
Chapuisia Dugès.

GENERA DESCRIBED IN 1911–12, NOT INCLUDED IN FOREGOING LIST, BUT HERE PROVISIONALLY ASSIGNED TO THE SUBFAMILIES.

Cyclorhipidion Hagedorn	Cryphalinæ.
Xyleborites Wickham	Do.
Pseudothamnurgus Eggers	Do.
Neotomicus Fuchs	Ipinæ.
Xestips Hagedorn	Do.
Pityokteines Fuchs	Do.
Trigonogenius Hagedorn	Do.
Allarthrum Hagedorn	Micracinæ.
Acacicis Lea	Hylesininæ.
Hapalogenius Hagedorn	Do.
Hylesinosoma Lea	Do.
Chætophorus Fuchs	Do.
Ficicis Lea	Do.
Minulus Eggers	Hexacolinæ.
Mesoplatypus Strohmeyer	Platypodinæ.
Notoplatypus Lea	Do.

GENERA OF DOUBTFUL POSITION.

Mesoscolytus Blndfd.
Phthorophlœus Rey.
Hyloscyllus Schauff.
Dendrotrupes Broun.
Styphlosoma Blndfd.
Acrantus Broun.
Inosomus Broun.
Araptus Eichh.

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NOTE.—The next contribution toward this monograph, entitled "Preliminary Classification of the subfamily Cryphalinæ, with descriptions of new genera and species," will be published as Report No. 99, Office of the Secretary, U. S. Department of Agriculture.

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